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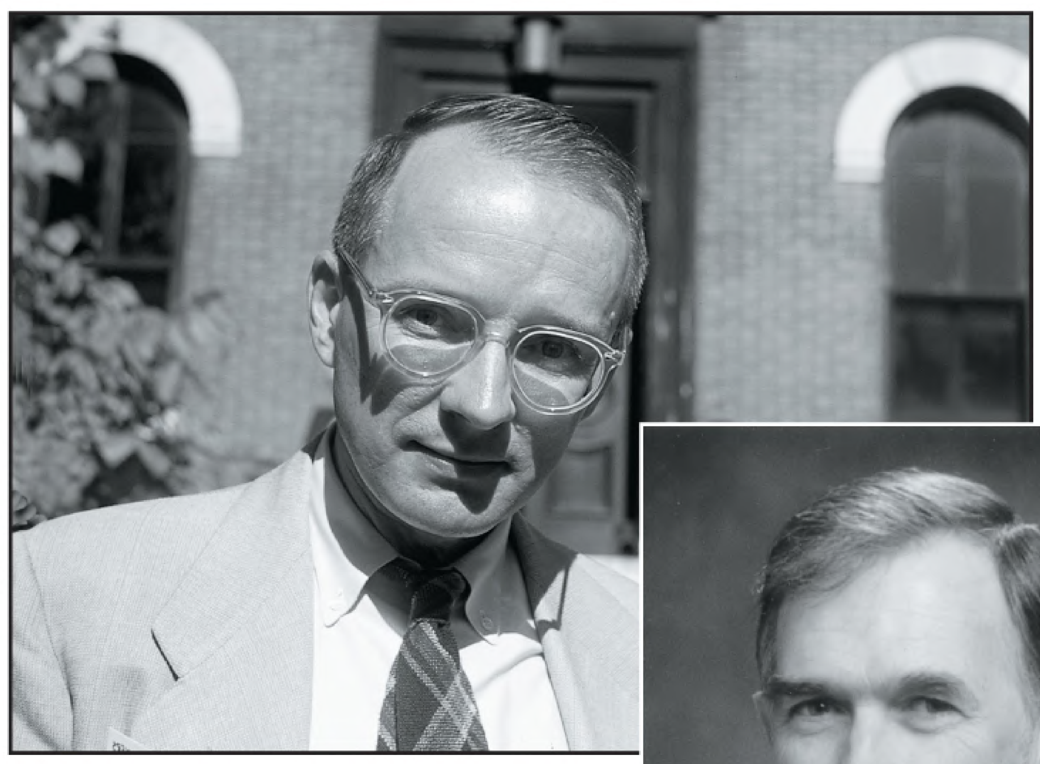

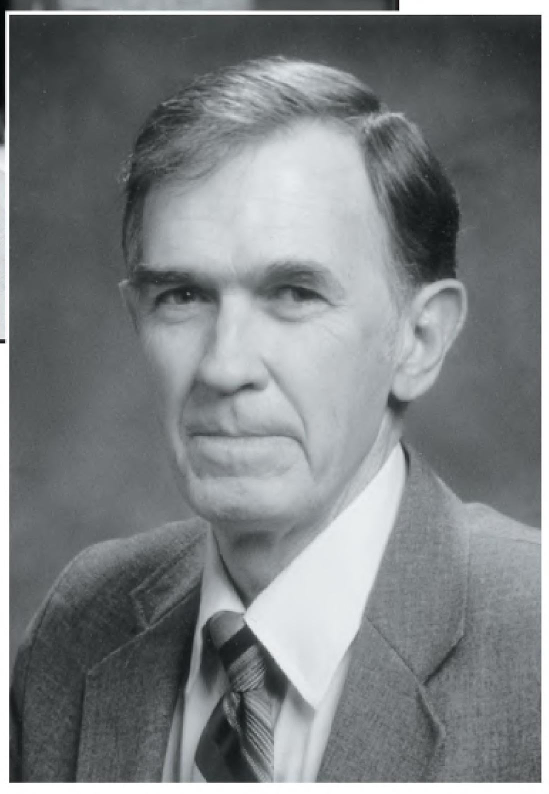

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A NEW *PHEMERANTHUS* (PORTULACACEAE) FROM THE PIEDMONT OF VIRGINIA AND NORTH CAROLINA

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ABSTRACT

Phemeranthus piedmontanus Ware, sp. nov. (Portulacaceae) is described from mafic and ultramafic rock outcrops in the Piedmont of Virginia and North Carolina, U.S.A. It differs from *P. teretifolius* in having more stamens that are much shorter than the style and in having a subcapitate stigma, and from *P. mengesii* in having fewer stamens and in being much smaller throughout. In crossing experiments, it did not hybridize with either of these species.

RESUMEN

Phemeranthus piedmontanus Ware, nueva especie (Portulacaceae), se describe de afloramientos de rocas máficas y ultramáficas en el pie de monte de Virginia y North Carolina, U.S.A. Esta especie difiere de *P. teretifolius* por tener más estambres, todos más cortos que el estilo, y por tener un estigma subcapitado. Difiere de *P. mengesii* por tener menos estambres y por su tamaño más pequeño en todo. En experimentos de hibridación, no hibridó con las dos otras especies.

INTRODUCTION

Only two species of *Phemeranthus* Raf. have been previously recognized from east of the Appalachians. They and all other eastern United States species were first described in the genus *Talinum* Adans. and have been treated under that name in all but the most recent literature (Kiger 2003). *Phemeranthus teretifolius* (Pursh) Raf., with a style about the same length as the 15–20 stamens, occurs in rock outcrop communities from the serpentine barrens of Pennsylvania and Maryland southward through the granitic and gneissic outcrops of the Piedmont from Virginia to Georgia. It also occurs on sandstone outcrops of the Ridge and Valley in Virginia and Tennessee (Ware & Pinion 1990; Murdy & Carter 2001; Kiger 2003) and on mafic and ultramafic outcrops in the western Piedmont of Virginia and North Carolina (C. Ludwig & A. Weakley, pers. comm.). *Phemeranthus mengesii* (W. Wolf) Kiger, with larger flowers than *P. teretifolius* and a style noticeably longer than the very many (50+) stamens, was first described from sandstone in the Ridge and Valley of Alabama (Wolf 1920, 1939), but also occurs on sandstone in the Ridge and Valley of Tennessee and in the Altamaha Grit region of Georgia (Montgomery & Blake 1969; Murdy & Carter 2001; Kiger 2003) and occasionally on granite (Carter & Murdy 1986).

Producing good herbarium specimens of species in this genus is made especially difficult by a combination of very delicate, ephemeral flowers coupled with thick succulent leaves and large, extremely firm rhizomes (Holzinger 1900; Ware 1967). Species can usually be distinguished by a variety of floral characters visible in fresh specimens with open flowers (such as petal color, petal shape, style color, stigma shape, filament color, and pollen color), but most of these characters are obscured in most herbarium specimens. As a consequence, identifications of herbarium specimens from east of the Appalachians have been based largely on stamen numbers (few versus many) and on whether the style is longer than or the same length as the stamens. Herein is described a new species of *Phemeranthus* that is like *P. mengesii* in having a style longer than the numerous stamens, but with a much smaller flower size and various other floral and habit characters that distinguish it both from that species and from *P. teretifolius*, as well as from other *Phemeranthus* species in the eastern United States.

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Phemeranthus piedmontanus Ware, sp. nov. (**Fig. 1**). Type: VIRGINIA. Franklin Co.: Bald Knob, Rocky Mount, collected from expansive metabasalt knob on treeless portions of the s-facing slopes of the Knob, plants abundant in mats scattered over 20 acres, 1 Aug 2007, *Ludwig 5051* (holotype: UNC; isotypes: to be deposited at NY, VDB [at BRIT], WILLI).

Similis Phemerantho mengesii sed parvior omnino; rhizoma plerumque multiramis et ergo multicaulibus; petala colore magis purpureo-rosea, plerumque quinque sed interdum quattor in eadem planta; stamina 20–35(–42), plerumque erecta, longitudine 2/3 styli partes aequantia; stigma parvum, subcapitatum; semina parva, atra.

Glabrous herb perennating by a usually multi-branched rhizome at the soil surface; roots fibrous, elastic; stems usually several, with a lower succulent part bearing many leaves, narrowing abruptly above to a leafless wiry stalk branching to become the inflorescence, to 15 cm long. Leaves many, terete, fleshy, to 4 cm long. Inflorescence cymose. Flowers regular, ephemeral, opening in the afternoon, closing before dusk. Petals pink, usually five, occasionally four on the same plant; sepals two, deciduous. Stamens usually 20–35(–42), often about 28, mostly erect, about 2/3 as long as style; pollen orangish. Style longer than stamens, upper 2/3 usually white, with small, white, subcapitate stigma; capsule ovoid to obovoid, 3–5 mm long, unilocular, dehiscing by three valves beginning at apex; placentation free central; mature seeds 10–25, smooth, black, about 0.6 mm long. Found in shallow soil on and around mafic (metabasalt, metagabbro, diabase) and ultramafic (including serpentine) rocks, Piedmont of Virginia (Franklin Co.) and North Carolina (Granville Co.). Flowers June through September.

The rock outcrops at the type locality on Bald Knob at Rocky Mount, Franklin Co., Virginia, were noticed by botanists long ago, but it was assumed that the *Phemeranthus* was *P. teretifolius*, then the only species reported from Virginia (Wherry 1936). The new species is also known from three additional locations in Franklin Co., Virginia, and a single location in North Carolina. Alan Weakley of the University of North Carolina first recognized that plants from the diabase glade at Butner, Granville Co., North Carolina were distinct from *P. mengesii* while working on his key to the flora of the Carolinas and Virginia. He eventually included these plants in his on-line key as an unnamed entity. Independently, Chris Ludwig of the Virginia Division of Natural Heritage discovered that plants from Franklin Co., Virginia did not fit either *P. teretifolius* or *P. mengesii* in Weakley's then-current keys and contacted Weakley about it. The two of them then called the plant to my attention and invited me to explore its relationships and describe it as a new species if I agreed with them on its distinctiveness.

Other specimens examined: **NORTH CAROLINA. Granville Co.:** *Weakley 7501* (UNC), diabase glade along B Street, Butner. **VIRGINIA. Franklin Co.:** *Ludwig 1440; Ludwig 2338; Ludwig 2339; Belden 268* (all at Virginia Natural Heritage).

MATERIALS AND METHODS

Common Garden Observations.—Over 50 plants of the new species were transplanted into pots in their native soil, and their growth and form were observed over seven growth seasons outdoors at Williamsburg, Virginia. For six years, plants of four other species (also in pots of their respective soil types) were grown alongside the new species, allowing comparisons of growth and form and tests for cross-pollination.

Cross-Pollinations.—Reciprocal crosses were carried out between Franklin Co., Virginia plants of *P. piedmontanus* and several other eastern North American *Phemeranthus* species, including *P. mengesii* from Marion Co., Alabama sandstone outcrops; *P. calcaricus* (Ware) Kiger from Rutherford Co., Tennessee limestone outcrops; and *P. calycinus* (Engelm.) Kiger from three locations: a Barry Co., Missouri limestone outcrop; an Izard Co., Arkansas sandstone outcrop; and a Montgomery Co., Arkansas shale outcrop. When the style exceeds the stamens, as in all but *P. teretifolius*, emasculation of the pistillate parent before hand-pollination is not necessary; with sufficient care, the cluster of stamens from the staminate parent usually can be used to brush pollen on the protruding style without disturbing the stamens of the recipient. *Phemeranthus teretifolius* from Powhatan Co., Virginia granite outcrops was used as a staminate parent but not as a pistillate parent because of the difficulty of dissecting out its stamens before anther dehiscence (and self-pollination) takes place.

Herbarium specimens.—About 90 herbarium specimens of *Phemeranthus* from Virginia and North Carolina (UNC, WILLI) were examined to try to find additional populations of the new species.

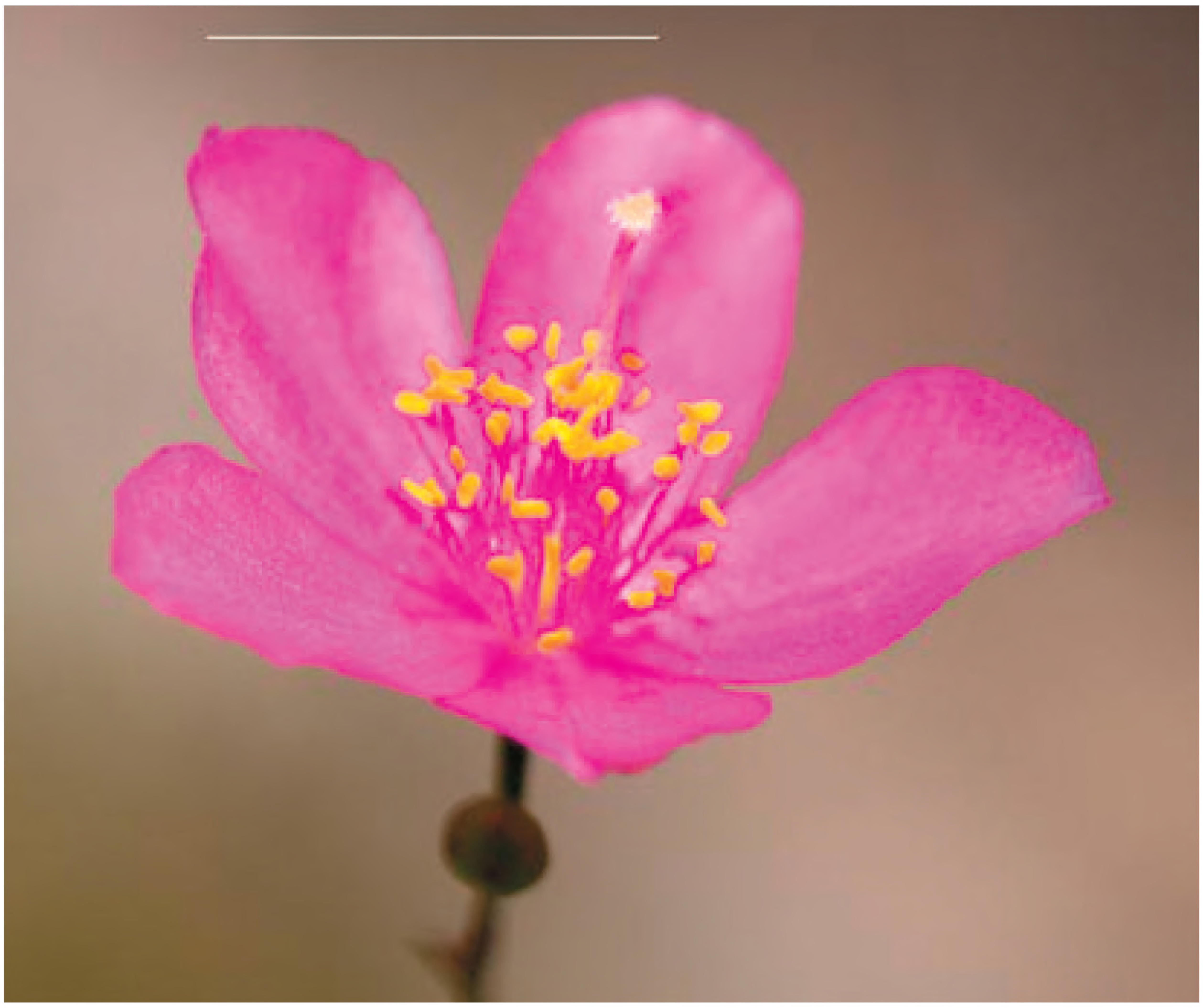

Fig. 1. Fully open flower of *Phemeranthus piedmontanus*. The line above the flower equals 1 cm.

RESULTS AND DISCUSSION

Field and Common Garden Observations.—In the field, one can observe a number of morphological differences that distinguish mature *P. piedmontanus* plants from other eastern and southeastern species in this genus, but many of these characteristics are not easily discerned in herbarium specimens. These characters are discussed below, and major ones are presented in Table 1.

Phemeranthus plants grow very slowly in nature; young plants of any species may have a linear, semi-erect rhizome and single above-ground stem for several years and may begin to flower even before the final mature rhizome form is achieved. However, mature rhizomes of *P. piedmontanus* are usually multi-branched from a central core, the rhizome branches extending above the soil level during winter and each giving rise to one or two stems in spring, producing a multi-stemmed plant. This is similar to the growth form of mature *P. calycinus* of sandstone and shale outcrops in Arkansas, but contrasts with most mature plants of *P. mengesii* and *P. teretifolius* and with *P. calcaricus* of limestone outcrops in Tennessee and Alabama, all of which normally have irregularly tuberous rhizomes at the soil surface with only a few stems arising from a rhizome.

In seven years of observation, none of over 50 plants of *P. piedmontanus* produced any vegetative propagules as the stems went dormant in the fall, either from the fleshy lower part of the stem, as is common in both *P. teretifolius* and *P. calcaricus* (Harshberger 1900; Ware 1967, 1969b), or within the inflorescence, as has been described for some more eastern populations of *P. mengesii* (Carter & Murdy 1986). The presence or lack of vegetative reproduction is rarely evident in herbarium specimens because these vegetative propagules are detectable only as the plants go dormant in the fall.

In North Carolina at Butner Glade, where *P. piedmontanus* and *P. teretifolius* occur together on the

Table 1. Differences between *P. piedmontanus* and similar eastern *Phemeranthus* species.

Species	***P. piedmontanus***	***P. mengesii***	***P. teretifolius***	***P. calcaricus***
Stamen Arrangement	mostly erect	spreading to erect, forming "dome"	erect	mostly erect
Erect Stamen Length	⅔ to ¾ length of style	¾ to ⅚ length of style	as long as style	¾ length of style
Stamen number	20–35(–42), often ± 28	50–90	15–20	25–45
Pollen color	orange or golden	yellow	yellow	yellow
Stigma	subcapitate, white	subcapitate, white	three-lobed, white or pinkish	three-lobed, white or pinkish
Normal petal number	5 or 4	5	5	5
Petal width-length ratio	more than ½ as wide as long; when 5, lower ¼ of petals clearly over-lapping when fully open	about ½ as wide as long; lower ¼ of petals slightly or not at all overlapping	about ½ as wide as long, lower ¼ of petals not overlapping or barely so	about ½ as wide as long, lower ¼ of petals not overlapping or barely so
Petal angle when fully open	curved upward & slightly elevated, forming broad, open "cup"	horizontal to slightly elevated	horizontal to slightly elevated	horizontal to slightly elevated
Petal length	6–10 mm	9–12 mm	5–8 mm	8–10 mm
Petal color	rich purplish-pink	rich pink	rich purplish-pink	darker purplish-pink
Sepals	deciduous	deciduous	deciduous	persistent
Seeds	small, black	small, black	small, black	larger, gray
Outcrop types	mafic and ultramafic rocks	mostly sandstone, but also granite	mostly granite & gneiss, but also sandstone and mafic & ultramafic rocks, incl. serpentine	limestone

same diabase outcrop, leaves of *P. piedmontanus* appear shorter on average than those of *P. teretifolius* (Alan Weakley, pers. comm.). However, there is much overlap of actual leaf length, which varies considerably in both species, so leaf length is not a reliable key character for separating the species.

The petals of *P. piedmontanus* are much smaller than those of *P. mengesii* and are about the same length and somewhat wider than those of *P. teretifolius*. They are a more intense pink than in *P. mengesii* and are the same color or slightly more intense pink than in *P. teretifolius*, but a lighter pink than in *P. calcaricus* from west of the Appalachians. Most flowers have five petals, but some *P. piedmontanus* plants produce both five-petaled and four-petaled flowers, with the latter apparently normal otherwise. In the five-petaled flowers, the lower ¼ to ⅓ of adjacent petals strongly overlap, and the petals curve upward and are usually slightly elevated when the flowers are fully open. In other eastern species, the petals are more nearly horizontal when fully open, and adjacent petals usually overlap only slightly or not at all. All these petal characters except size are often lost in pressing.

The 20–35(–42) stamens of *P. piedmontanus* are mostly erect, with the stamens nearest the style about ⅔ as long as the style. This difference in stamen and style length prevents pollination without a vector. This androecium contrasts with the more spreading and more numerous (usually 50+) stamens of *P. mengesii*, which form a "dome" or "brush," with the more erect stamens nearest the style about ¾ to ⅘ as long as the style. This difference in the degree of spread of the stamens is often lost in pressing. The pollen is orangish or golden in *P. piedmontanus*, as opposed to yellow in *P. mengesii* and other eastern species, although this difference may be obvious only when two species are looked at side by side. In *P. teretifolius*, the fewer (<20) but erect stamens are as long as or slightly longer than the style. This shorter style holds the stigma at

Table 2. Results of crosses between *Phemeranthus* species.

Pistillate parent	Staminate parent	Number of pollinations	Number of producing capsules	Number of normal-appearing seeds/ capsules
P. piedmontanus	*P. mengesii*	10	0	–
P. mengesii	*P. piedmontanus*	10	3	0; 1; 3
P. piedmontanus	*P. teretifolius*	10	0	–
P. piedmontanus	*P. calcaricus*	10	0	–
P. calcaricus	*P. piedmontanus*	10	0	–
P. piedmontanus	*P. calycinus* from AR SS	10	0	–
P. calycinus from AR SS	*P. piedmontanus*	10	0	–
P. piedmontanus	*P. calycinus* from MO LS	10	0	–
P. calycinus from MO LS	*P. piedmontanus*	10	0	–
P. piedmontanus	*P. calycinus* from AR shale	10	0	–
P. calycinus from AR shale	*P. piedmontanus*	10	0	–

the same level as or slightly below the anthers, allowing pollination as the flower closes, so a vector is not essential for fruit set, while a vector is needed in *P. piedmontanus*.

The subcaptitate stigma and usually the upper ⅔ of the style are white in both *P. piedmontanus* and *P. mengesii*, but both style and stigma are much smaller in the former. In contrast, *P. teretifolius, P. calcaricus*, and all populations I have seen of *P. calycinus* have strongly tripartite stigmas, and usually (but not always) have pink pigment in the upper style and sometimes even where the three branches of the stigma join.

This genus is renowned for strong synchrony and predictability of daily opening and closing of flowers, and flowering time has been invoked as a way to separate species (Holzinger 1900). However, daily flowering time may vary among populations of the same species, may coincide in two different species, and at any location varies with daily cloudiness and portion of the growth season (Ware 1967; Ware 1993), so it must be used with caution. Plants from Bald Knob at Rocky Mount, Virginia usually open around 1:30–1:45 pm EDT and close about 5:30. This contrasts with most Virginia populations of *P. teretifolius*, which flower later (often around 3:30 EDT) and stay open later. Earlier opening of flowers in *P. piedmontanus* also occurs where it and *P. teretifolius* occur on the same outcrop in North Carolina (A. Weakley, pers. comm.).

Crossing Attempts.—All self-pollinations produced normal fruit filled with normal-appearing seeds. None of the cross-pollinations could be called successful. Only three pollinations caused capsules to form, all when *P. mengesii* was the pistillate parent and *P. piedmontanus* was the staminate parent (Table 2). In one of these capsules, no normal seeds were produced, and only one and three normal-looking seeds were produced in the other two capsules, far below the 25 to 50 seeds produced in manually self-pollinated *P. mengesii* plants. No attempt was made to germinate the four normal-appearing seeds, but such a low fruit set and such a small number of normal-appearing seeds clearly indicate strong barriers to cross-pollination. Further, accidental self-pollination of *P. mengesii* during the crossing efforts cannot be ruled out completely.

Herbarium Specimens.—No specimens from additional locations in North Carolina or Virginia could be surely identified as *P. piedmontanus*. The floral characters used to distinguish this species in life are poorly preserved in most collections. Almost no specimens had been pressed during the afternoon hours when flowers are fully open. Herbarium labels rarely gave information about relative style/stamen length or whether stamens were few or very many. In a few specimens with a closed flower that had been open on the day of collection, dissection can allow assessment of the relative length of style and stamens and tentative counts of stamens, but such dissection destroys the flower, eliminating evidence for future confirmation of identity. *Phemeranthus* specimens should be pressed in the afternoon while flowers are fully (not partially) open, and labels should include notes on the relative length of style and stamens, whether the stamens are many or relatively few, and preferably an actual count of stamens in at least one flower.

Ecology.—*Phemeranthus piedmontanus* seems to play essentially the same ecological role on mafic and ultramafic outcrops in Virginia that other *Phemeranthus* species play in their respective habitats in eastern North America (Ware 1969a, 1969b). However, it does not monopolize these substrates; searches of neighboring mafic and ultramafic outcrops for other populations of the new species have found only *P. teretifolius* (C. Ludwig, pers. comm.), and the two species co-occur on the diabase substrate of Butner Glade in North Carolina (A. Weakley, pers. comm.). Even though the soil where this new species has been found is mafic to ultramafic, at the type locality common associates (C. Ludwig, unpublished data) include species typical of shallow soil on non-mafic granite and sandstone outcrops, such as *Minuartia glabra* (Michx) Mattf., *Hypericum gentianoides* (L.) B.S.P., *Saxifraga virginiensis* Michx., *Selaginella rupestris* (L.) Spring, and *Nuttallanthus canadensis* (L.) D.A. Sutton (McVaugh 1943; Palmer 1970; Berg 1974; Wyatt & Fowler 1977; Houle 1987; Quarterman et al. 1993; Belden 1998). Associates at the type locality do not include typical limestone outcrop species, such as *Isanthus brachiatus* (L.) B.S.P. (= *Trichostema brachiatum* L.), which is among the species found on the diabase outcrop in Granville Co., North Carolina (Le Grand 1988). Experiments are planned on the relative growth rates of *P. piedmontanus* on its own native mafic substrate and on soil from non-native granite and limestone outcrop soils, as has been done previously for other *Phemeranthus* species (Reinhard & Ware 1989; Ware & Pinion 1990).

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BOOK REVIEWS

Julia A. Jordan. 2008. **Plains Apache Ethnobotany.** (ISBN 978-0-8061-3968-5, hbk.). University of Oklahoma Press, 2800 Venture Drive, Norman, Oklahoma 73069-8216, U.S.A. (**Orders:** www.oupress.com/; 1-800-627-7377). $34.95, 212 pp., 22 photographs, 1 map, 9¼" × 6 ¼".

Little ethnobotanical research has been done on the indigenous peoples of the Southern Plains, and this work provides a valuable contribution to the literature.

The book was published in 2008; however, the field work among the Plains Apache (also known as the Kiowa Apache) was done in the early 1960s for the author's master's thesis research.

Six elders were interviewed and accompanied the author to various sites where the plants were known to grow. The plants were identified and collected and various stories were recorded. The work is important since many of the informants are no longer living, and their knowledge represents a generation of Plains Apache that span the times of settlement into reservations through modern times. This research documents plant usage from people living from the 1890s to 1950s.

The book is organized into two main parts. Part One provides historical and cultural background of the Plains Apache. Part Two details the plants utilized by the Plains Apache for food, medicine, ritual uses, material culture, firewood, personal care, and adornment. The entries for each plant include common names in English, names in the Plains Apache language and translations, and much detail about the manner in which the plant was collected, prepared, and used.

The botanical nomenclature has been updated to the standard of the USDA Plants Database. The book includes photographs, bibliographic references, an index, and tables of the plants used by the Plains Apache.

Overall, the book consists of quality research and sound writing; however, I noticed one factual error. The author lists Sitting Bull as Arapaho, when in fact he was Hunkpapa Lakota. But this issue is minor and does not detract from the overall value of the book.

Overall, this book is well-organized, full of interesting anecdotes, and is an important and invaluable reference to anyone interested in traditional environmental knowledge, lifeways of the Native Americans, or useful plants of the Southern Plains. It contributes to the documentation of endangered knowledge that is largely being lost to the passing of the generations.—*Brian Boe, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

Peter Mickulas. 2007. **Britton's Botanical Empire: The New York Botanical Garden and American Botany, 1888–1929.** (ISBN-13:978-0-89327-479-5, 10:0-896327-479-8, hbk.). *Memoirs of The New York Botanical Garden, Vol. 94.* The New York Botanical Garden Press, 200th Street & Kazimiroff Boulevard, Bronx, New York 10458-5126 U.S.A. (**Orders:** www.nybgpress.org; 718-817-8721). $45.00, 316 pp., b/w photos, 10¼" × 7¼".

Britton's Botanical Empire: The New York Botanical Garden and American Botany, 1888–1920 is both a history of botany and horticulture in New York City during the Gilded Age and a biography of the man who made the vision of the garden happen, Nathaniel Lord Britton.

The idea for the New York Botanical Garden supposedly began in 1888 when Britton visited Kew Gardens on his honeymoon. His new wife asked, "Why couldn't we have something like this in New York?" The book chronicles the next thirty years as both Nathaniel Britton and his wife Gertrude Knight Britton work to fulfill their vision of a garden suitable for the nations' commercial capital.

This is a very detailed account of those years as Britton works with a coalition of New York philanthropists and scientists, navigating through rivalries and politics to change a piece of park land in the Bronx into an urban garden, enjoyed by city dwellers, as well as a venue for botanical science. The role of the garden in the cultural development of New York City is examined as well many other aspects such as garden design and the operation of public gardens.

In addition to the story of the Garden, Britton's career as botanist is examined. He worked to raise the study of botany to the level of chemistry or physics and to have American botanists seen as the authority on the Western Hemisphere. He mounted expeditions to survey the flora of Puerto Rico and participated in a decades long dispute over taxonomic nomenclature.

Mickulas' history of Britton would appeal to those readers interested in the history of science and the history of botany and horticulture.—*Pam Braak, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

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A NEW HEDGE-NETTLE (*STACHYS*: LAMIACEAE) FROM THE MID-ATLANTIC PIEDMONT AND COASTAL PLAIN OF THE UNITED STATES

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ABSTRACT

A new, geographically restricted "hedge-nettle," **Stachys matthewsii** (Lamiaceae) is described from the region that includes southeastern and south-central Virginia and north-central North Carolina. This taxon resembles *Stachys latidens* Small ex Britton, a species of higher-elevation forests of the Blue Ridge Mountains, but has consistent morphological differences in stem pubescence and has distinctly different habitat requirements. Two keys are provided for distinguishing hedge-nettles of the southeastern United States.

ZUSAMMENFASSUNG

Zur Beschreibung des neuen Ziests, **Stachys matthewsii** (Lamiaceae), lässt sich sagen, dass seine geographische Verbreitung auf den südöstlichen und den mittleren Süden Virginias und den mittleren Norden North Carolinas begrenzt ist. Die neue Art ähnelt *Stachys latidens* Small in Britton, einer Pflanze aus den höher gelegenen "Blue Ridge Mountains," aber sie hat konsistente morphologische Unterschiede in der Stammpubeszenz und hat völlig andere Habitat-Ansprüche. Zwei Schlüssel dienen zur Bestimmung der Ziest-Arten aus den südöstlichen USA.

RESUMEN

Se describe una nueva "ortiga muerta," **Stachys matthewsii** (Lamiaceae) restringida geográficamente a la región que incluye el sureste y sur-centro de Virginia y norte-centro de Carolina del Norte. Este taxon se parece a *Stachys latidens* Small ex Britton, una especie de los bosques a mayor elevación de las montañas del Blue Ridge, pero tiene diferencias morfológicas consistentes en la pubescencia del tallo y distintos requerimientos de hábitat. Se aportan dos claves para diferenciar las xxx del sureste de los Estados Unidos.

INTRODUCTION

Field work and herbarium studies in North Carolina and Virginia has led to the circumscription of a new species in the genus *Stachys*, a large group of mints widely recognized for its taxonomic complexity. Changing taxonomic interpretations in the past have confounded efforts to classify this plant properly, but enough has now been learned to recognize this species' unique place within the genus. A history of taxonomic opinions regarding *Stachys matthewsii* is presented, as is a discussion of habitat and geography, particularly its primary range in the Piedmont and its somewhat disjunct Coastal Plain populations in Virginia.

Stachys matthewsii G.P. Fleming, J.B. Nelson, & J.F. Townsend, sp. nov. (**Figs. 1–5**). Type: UNITED STATES: North Carolina. Montgomery Co.: fairly shady woodland on E side of Yadkin River, just downstream from Falls Dam, Uwharrie National Forest, 11 Jun 1979, *John B. Nelson 1152 with J. Matthews* (holotype: USCH; isotypes: FSU, MO, NCU, UNCC[2]).

Differt a *Stachys latidens* ob trichomata longa expansaque ad caulis angulas. Differt a *Stachys hispida* ob calycis lobos breviores et minus deltatos pro parte. Differt a *Stachys cordata* ob folia parviora, minus cordata, et petiolos breviores. Differt a *Stachys nuttallii* ob caulis facies leves.

Perennial **herbs** from vigorous, pale, fragrant rhizomes; flowering **stems** erect, 0.8–1.05m tall, sparingly branched, even within inflorescence, or branched toward base on older plants; the sides glabrous as high as the lowest verticil, fertile internodes with scattered short glandular hairs, the angles prominently and consistently pubescent with stiffish, spreading (or retrorse) hairs, these eglandular, to 3mm long; nodes bearded with hairs as those on the stem angles; the overall pubescence is dense at the base of the plant, becoming progressively less so upwards; **leaves** consistently petioled, the petioles 2–5mm long, blades mostly rounded at base or somewhat cordate, the blades 5–10 cm long, 2–5cm broad, broadly elliptical to lance-ovate, acute

at apex, the margins crenate (crenulate-serrulate), leaves spreading-ascending, upper surface prominently bullate, abundantly pubescent with appressed and erect non-glandular, pustulate-based hairs, the lower surface glabrate to softly pubescent with erect, eglandular hairs; **inflorescences** of interrupted verticils; **bracts** abruptly reduced upward from lowest fertile nodes; **cymules** each with 3 flowers, the verticils thus 6-flowered; fruiting **calyces** campanulate, the tube densely short-soft pubescent, and with longer, stiffish hairs, especially along the veins, and slightly atomiferous-glandular, tubes mostly 4mm (3.5–4.5mm) long; the lobes deltoid, narrowed apically and terminated with minute apiculum, the lobes less than one-half the length of the tube, 1.5–1.8(–2.4)mm long; **corollas** pink, corolla tube prominently saccate toward base on lower side, tube internally glabrous, but with prominently slanting (oblique) annulus, copiously pubescent with soft, bulbous trichomes; tube 11–14mm from base to apex of galea; galeae abundantly pubescent with stalked glands and soft eglandular hairs; lower lip with prominent dark pink (nearly purple) blotches on the median portion of the lower lip; declined to 90° from the tube, 6.5–8mm long, the middle lobe of lower lip narrowly ovate, slightly notched at apex; **mericarps** dark brown, minutely pebbled, 1.4–1.5mm wide, 1.8–2mm long.

Additional collections examined: **UNITED STATES. VIRGINIA. Amelia Co.:** local in wet meadows and old fields, 5 Jul 1938, *J.B. Lewis 1592* (FSU). **Brunswick Co.:** along wooded stream, Jun 1942, *J.B. Lewis 3588* (VPI). **Charlotte Co.:** young floodplain forest along Cargills Creek, 3.5 mi E of Dryburg, 14 Aug 2008, *Gary P. Fleming 15453 with John F. Townsend* (VPI). **Halifax Co.:** moist swale in powerline clearing 2.2 mi SW of Public Fork, 14 Jul 1995, , *Gary P. Fleming 10804* (GMUF, USCH, VPI, WILLI); same location, 1 Jul 1997, *Gary P. Fleming 13418* (UNC, US); same location, 14 Aug 2008, *John F. Townsend 4061 with Gary P. Fleming* (VPI); thinly wooded toe slope along Staunton River, 0.6 mi. south of US 360 bridge and 2.3 mi. west-southwest of Public Fork, 26 May 2010, *Gary P. Fleming 15470* (VPI). **Pittsylvania Co.:** dry woodland edges (rich), 22 Jun 1963, *W. Hathaway s.n.* (LYN); sandy bottomland, county road #608 near Pigg River, 25 Jun 1966, *W. Hathaway s.n.* (LYN); below bridge over Staunton River on [US] Hwy 29 across from Altavista, 29 Jun 1966, *G. Ramsey s.n. et al.* (LYN); old jeep trail in woods on west side of US 29 bypass on south side of Staunton River, 2 river mi. upstream from Alta Vista, 30 Jul 1994, *John B. Nelson 16019* (GH, USCH). **Surry Co.:** rich alluvial woods and thickets back of sand-beach of James River, below Sunken Meadow Beach, 14 Jun 1938, *M.L. Fernald and B. Long 8446* (GH); thicket back of sand-beach of Cobham Bay, James River, northwest of Chippokes, 25 Aug 1940, *M.L. Fernald and B. Long 12788* (GH); sandy river bank, southeast of Claremont, 25 Jun 1950, *B. Mikula 5514* (FARM, WILLI). **NORTH CAROLINA. Durham Co.:** wooded pasture, northeast of Durham on Neuse River at Co. line (SW of Cozart), 21 Aug 1965, *Harry E. Ahles 59795* (NCU). **Granville Co.:** disturbed right of way, former Seaboard Coastline RR bed 0.2 mi SW of SR 1726, 28 Jun 2006, *Dale E. Suiter 2505 et al.* (NCU). **Montgomery Co.:** same location as type, 21 Jun 1978, *J. Matthews et al. s.n.* (UNCC); 16 Jun 1998, *H. Selvig s.n.* (USCH); 23 Jun 1988, *J. Nelson 6733* (USCH).

DISCUSSION

The earliest known collections of *Stachys matthewsii* were made by Fernald and Long in 1938 and 1940, during their exploration of unusual, shell-rich, calcareous bluffs and shores along the James River in the southeastern Virginia Coastal Plain (Fernald 1938, 1941). Fernald initially determined these collections as "*Stachys nuttallii* Shuttlew.," but later changed his diagnosis to "*Stachys clingmanii* Small," (Fernald 1943, 1950). Confusion in the interpretation of other historical collections of *S. matthewsii* is also evident, and is perhaps best epitomized by J.B. Lewis' 1942 collection from Brunswick County, Virginia. This specimen was originally labeled *S. tenuifolia* Willd., but was subsequently annotated between 1972 and 2005 as *S. clingmanii* Small, *S. nuttallii* Shuttlew. ex Benth., *S. eplingii* J.B.Nelson, and finally, *S. hispida* Pursh.

James Matthews' (UNCC) discovery of this plant in Montgomery County, North Carolina arose from an inventory of unusual habitats and rare species within the Uwharrie Mountains region. On June 21, 1978, Matthews collected two specimens of the hedge-nettle in question during a search for *Helenium brevifolium* (Nutt.) Wood, along the east side of the Yadkin River just below the Falls Dam. The plants were considered unusual and tentatively identified as *Stachys riddellii* House (= *S. cordata* Riddell). Nelson (then at FSU) was alerted to the presence of this unusual hedge-nettle by Matthews in 1979, and driven to the population for some observations. He later made trips to the same spot, again accompanied by Matthews, in 1988 and 1998. Between 1994 and 2008, new populations and/or herbarium specimens from four additional counties in south-central Virginia were located by Nelson, Fleming, and Townsend.

Conflicting determinations of historical specimens of *Stachys matthewsii* can be partly explained by the incomplete and evolving treatments of *Stachys* during the mid-20th Century, and partly by the lack of any

available key or description that would account for the particular combination of characters that are diagnostic of the taxon. In recent decades, interpretation of the genus has become more stable, with circumscriptions of native southeastern species generally based on combinations of three character-groups: relative petiole length, shape and relative length of the calyx lobes, and distribution and type of stem pubescence (Nelson 1981; Mulligan & Munro 1989). *Stachys matthewsii* is characterized by the combination of short petioles, short triangular-apiculate calyx lobes, and copious pubescence restricted to the stem angles (Figs. 2, 3, and 5). This taxon was not clearly recognized in any treatment until that by Nelson (1981), who maintained it within *S. nuttallii* (= *S. cordata*) as a short-petioled variant, disjunct from the rest of the range. Current treatments of the *nutallii-cordata* group, however, distinguish its members not only by their long-petioled leaves but also by the presence of hairs on the stem sides and their musky-scented, atomiferous-glandular foliage (Nelson 2008), all characters absent in *S. matthewsii*. Contemporary interpretation of *S. clingmanii* as a longer-petioled, high-elevation plant of the southern Appalachians has rendered Fernald's view of the Surry County hedge-nettles both taxonomically erroneous and phytogeographically improbable (Nelson 1981; Gleason & Cronquist 1991).

The treatment by Mulligan and Munro (1989) would place the collections of this taxon within *S. latidens* Small. Annotations of the holotype and one paratype of *Stachys matthewsii* (*Nelson 6733*), supplied by G.A. Mulligan in 1990, read "*Stachys latidens* Small, very close to"; the holotype additionally bears Mulligan's note "angles long erect hairs." Like *S. matthewsii*, *S. latidens* has short petioles and short deltoid calyx lobes. However, it is a relatively smooth plant with only scattered, pustulate, short-deflexed hairs on the stem angles. Additionally, the bearded nodes and abundant, prominently spreading, multicellular hairs of *S. matthewsii* will consistently separate it from *S. latidens*. Moreover, the two species have allopatric distributions and disparate ecological affiliations, with *S. latidens* a plant of higher-elevation forests and clearings in the Blue Ridge and *S. matthewsii* a plant of low-elevation clearings and edges in the Piedmont and Coastal Plain. This geographic and ecological separation of *S. matthewsii* and *S. latidens* would seem to preclude any biological interaction between the two taxa at present. Other species, such as *S. hispida* and *S. tenuifolia*, are occasionally found sympatrically with *S. matthewsii*, but no intermediates have been seen to suggest any current gene exchange among members of the group. The type of multicellular pubescence seen in *S. matthewsii* could possibly indicate some past kinship with *S. hispida*, although the distribution and density of these pustular-based, multicellular hairs is distinctly different in the two taxa. Specifically, *S. hispida* is more or less uniformly hispid with a moderate to somewhat dense concentration of hairs along the stem, whereas those of *S. matthewsii* are only moderately dense above but rapidly become very densely concentrated in the proximal 3–4 nodes and internodes. Without a molecular framework for placing the various species of *Stachys*, such morphological and ecological evidence will remain the most practical tools for recognizing new taxa in this complex genus.

The population at the type locality is near the margin of the Yadkin River, at the narrows just below (and within sight of) the Falls Dam, east of the town of Badin. The plants grow in considerable shade on sandy, loamy ground, with the population best developed on a somewhat sandy ridge. The site is probably best considered an occasionally flooded-scoured river levee complex. Associated species include *Liriodendron tulipifera* L., *Pinus echinata* Mill., *Liquidambar styraciflua* L., *Quercus nigra* L., *Robinia pseudoacacia* L., *Albizia julibrissin* Durazz., *Sassafras albidum* (Nutt.) Nees, *Alnus serrulata* (Aiton) Willd., *Amorpha fruticosa* L., *Parthenocissus quinquefolia* (L.) Planch., *Apios americana* Medik., *Vitis rotundifolia* Michx., and *Asplenium platyneuron* (L.) Britton, Sterns, & Poggenb., all of which are locally common and hardly indicating special or unusual habitats.

Subsequent study of populations and collections from Virginia demonstrate a wider distribution (Fig. 4). Most Virginia populations occur either along streams or in low, seasonally damp swales. Habitats could generally be considered mundane, except for those of the Surry County populations, which occupy calcareous open swales and forest edges along shell-laden shores of the James River. Repeated observations of populations in Halifax and Charlotte Counties indicate that *S. matthewsii* is quite shade-intolerant and not very

Fig. 1. *Stachys matthewsii* habit.

Fig. 2. Middle stem, leaves, and petioles of *Stachys matthewsii*.

Fig. 3. Flowering and fruiting calyces of *Stachys matthewsii*.

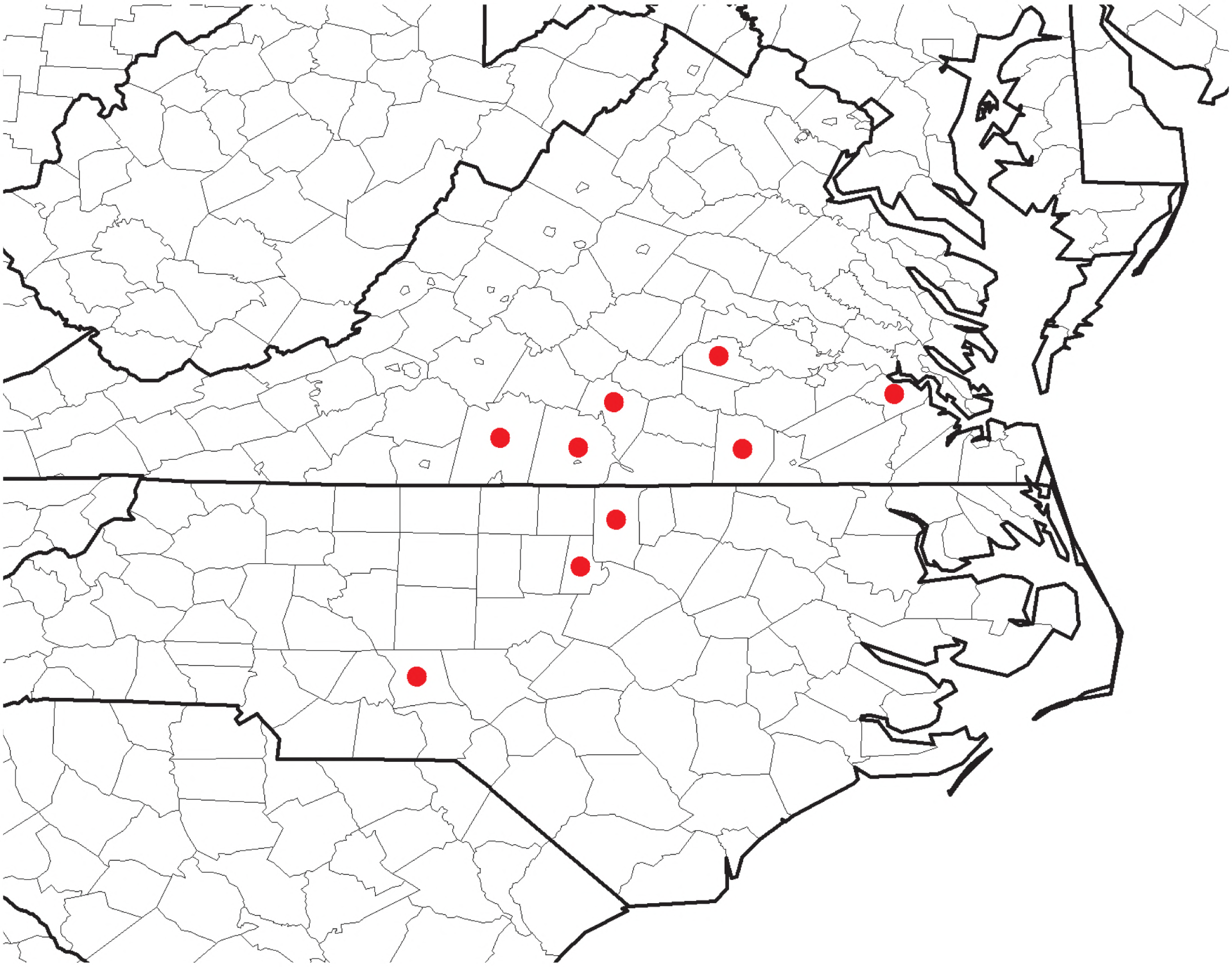

Fig. 4. County distribution of *Stachys matthewsii* specimens in Virginia and North Carolina.

competitive with taller, ruderal perennials. Plants growing in a formerly cleared floodplain now invaded by young trees have become progressively shade-stressed and do not flower. A periodically mowed powerline swale with short to medium-height herbaceous vegetation appears to represent optimal habitat for the species, supporting a population with hundreds of flowering plants. Perhaps the combination of shade-intolerance and poor competitive abilities, as well as low levels of botanical inventory in the Piedmont, accounts for the relatively low number of known populations, despite an abundance of seemingly suitable habitat in the region.

Notes on the Distribution of *Stachys matthewsii*

There is precedence for the somewhat disjunct distribution of populations of *Stachys matthewsii* between the North Carolina - Virginia Piedmont and calcareous habitats of the Virginia Coastal Plain. Previous investigations by Ware and Ware (1992) and MacDonald (2000) point to numerous species of primarily Piedmont and Mountain distribution with outlying populations in or adjacent to coastal ravine complexes underlain by the calcareous Yorktown and Eastover formations. These Pliocene deposits, due to their highly erodible nature, have allowed for the creation of relatively dramatic ravine complexes within the otherwise slightly undulating and acidic landscape of the Tidewater region. It is widely assumed that the disjuncts present in or near such ravines are relics of early Holocene climates, when species now confined to montane habitats were more broadly distributed in Virginia (Delcourt & Delcourt 1986). While *Stachys matthewsii* is not confined to these steep - sided erosional features, the presence of populations immediately adjacent to them on shelly substrates (and nowhere else in the region) certainly points to relictual distribution as a possible factor involved in their presence.

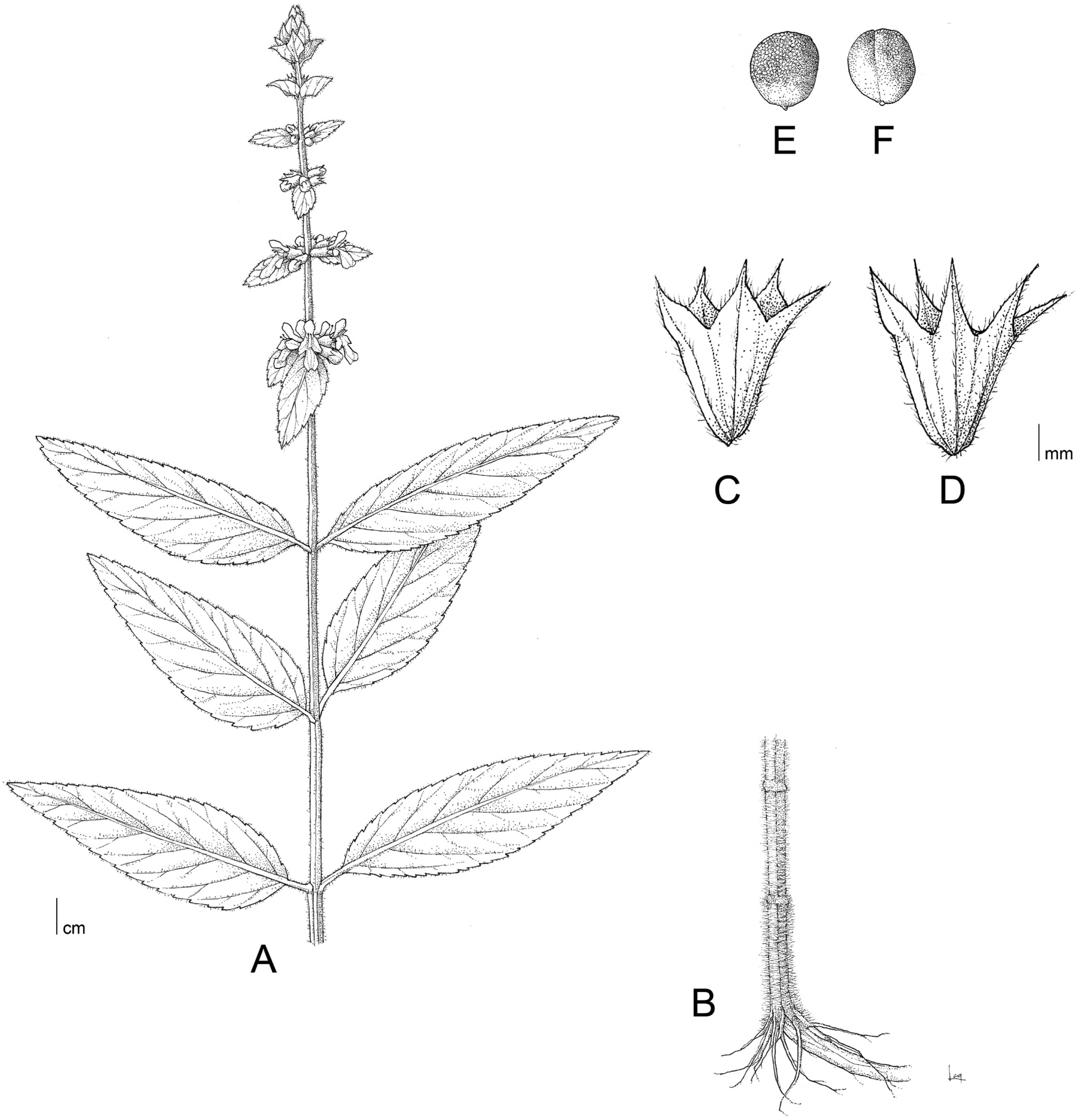

Fig. 5. *Stachys matthewsii* G.P. Fleming, J.B. Nelson, and J.F. Townsend. A. Habit, upper stem. B. Base of stem showing bearded nodes and densely hairy internodes. C. Calyx, *S. matthewsii*. D. Calyx, *S. hispida* (for comparison). E. Seed, dorsal view. F. Seed, ventral view (from *G.P. Fleming 13418*, NCU). Illustration by Lara Call Gastinger.

Numerous examples of this mountain/Piedmont–Coastal Plain disjunction type are described by Ware and Ware (1992) and MacDonald (2000), but the species *Scutellaria incana* Biehler and *Stewartia ovata* (Cav.) Weath. provide the best analogs for the distribution of *Stachys matthewsii* in Virginia. Each is found almost exclusively within the southern Piedmont of Virginia but have outlying populations within the coastal ravine systems discussed here.

Stachys matthewsii also belongs to a small group of species that have distributions centered in the southeastern Piedmont, sometimes extending into the adjacent inner Coastal Plain or to scattered disjunctions in the mountains. Five of these species are apparently endemic to Virginia and North Carolina: *Cardamine micranthera* Rollins, *Eupatorium saltuense* Fernald, *Hexastylis lewisii* (Fernald) Blomq. & Oosting, *Isoetes vir-*

ginica N. Pfeiff.and *Phemeranthus piedmontana* S. Ware (see Ware, this issue). Additional species that occupy a somewhat larger range, occurring primarily from southern Maryland or Virginia to South Carolina or northeastern Georgia, include *Clematis ochroleuca* Aiton, *Heuchera caroliniana* (Rosend., Butters & Lakela) E.F. Wells, *Hypericum lloydii* (Svens.) W.P. Adams, *Acmispon helleri* (Britton) A.A. Heller, *Phacelia covillei* S. Wats. ex A. Gray, *Rhus michauxii* Sarg., *Solidago pinetorum* Small, and *Symphyotrichum grandiflorum* (L.) G.L. Nesom. Several granite flatrock endemics that also fit this pattern include *Cyperus granitophilus* McVaugh, *Diamorpha smallii* (Britton ex Small), *Isoetes piedmontana* (N. Pfeiff.) C.F. Reed, and *Portulaca smallii* (P. Wilson).

Etymology

In presenting this new taxon, we have selected the epithet "*matthewsii*" as a way of honoring James F. Matthews, who initiated this process with his early collections, and who alerted Nelson to the potential issue. Jim's record as an outstanding botanist, teacher, and mentor is continued through his dedication to and support for the UNCC Herbarium; we are honored to recognize him in this way.

KEYS TO SOUTHEASTERN *STACHYS*

Building on the work of Nelson (2008), two field keys are provided to aid identification of *Stachys matthewsii* and the integration of this taxon into contemporary treatments of southeastern *Stachys*. The first key uses relative petiole length as the primarily character, while the second uses shape and relative length of the calyx lobes. The user may find that one key has greater utility with a given specimen, and that the use of two approaches is helpful in identifying difficult specimens.

KEY 1

1. Annual; corolla scarcely exserted from calyx ____ **S. agraria**
1. Perennial: corolla prominently exserted from calyx; widespread.
    2. Petioles obvious, those of the mid-stem leaves generally ⅕ as long as the leaf blades.
        3. Calyx tubes glandular.
            4. Leaf blade margins dentate or nearly so; stem angles copiously pubescent with long (to 3 mm), spreading hairs ____ **S. clingmanii**
            4. Leaf blade margins mostly crenate; stem angles glabrate or pubescent with mostly short, retrorse hairs.
                5. Leaf blades < 3 cm wide; plants weedy, scarcely 0.75 m tall, with white, rounded tubers terminating rhizomes ____ **S. floridana**
                5. Leaf blades commonly > 3 cm wide; plants not weedy, commonly 1 m or more tall; rounded tubers absent.
                    6. Leaf blades ovate, the bases cordate; margins crenulate ____ **S. cordata**
                    6. Leaf blades elliptic-oblong, the bases rounded to slightly cordate; margins crenate to serrate ____ **S. nuttallii**
        3. Calyx not glandular, or very slightly so.
            7. Calyx glabrous to sparsely pubescent; petioles well-developed, especially in shade forms ____ **S. tenuifolia**
            7. Calyx variously hairy, but at least hispidulous, frequently strongly hispid; petioles short or long.
                8. Petioles usually well developed; stem angles abundantly pubescent with spreading hairs; blade margins dentate ____ **S. clingmanii**
                8. Petioles short to nearly absent; stem angles commonly pubescent, with retrorse hairs; blade margins serrate ____ **S. hispida**
    2. Petioles short, those of the mid-stem leaves < ⅕ as long as the blades or absent.
        9. Leaves linear-lanceolate to narrowly lanceolate, usually widest at or near the base; leaf margins entire to crenulate, rarely serrulate, and then mostly towards the apex.
            10. Upper stem sides prominently pubescent; leaf blades abundantly pubescent below with appressed hairs, thus closely tomentose, the lower surface felty or velvety; corolla purplish; rarely adventive ____ **S. palustris**
            10. Upper stem sides glabrous; leaf blades variously pubescent or glabrate, but never felty nor velvety; corolla pink; native species
                11. Leaf blades narrow, 3–6 mm wide; plants generally glabrous to moderately pubescent; blade margins entire to obscurely crenulate ____ **S. hyssopifolia**

11. Leaf blades broader, 5–8 mm wide; plants frequently hispidulous or abundantly pubescent; blade margins crenulate to serrulate ____ **S. aspera**

9. Leaves ovate to elliptic or oblong, widest near the center or toward the apex; leaf margins crenate to sharply serrate for nearly the entire length.

12. Stem sides commonly pubescent above.

13. Calyx lobes lanceolate; flowers 6 per verticil; leaf margins serrate-crenate

14. Leaves generally subsessile, the petioles thick, not longer than 6 mm; blades densely pubescent, frequently soft-pilose or velvety; leaf margins serrate; VA and WV only ____ **S. arenicola**

14. Leaves generally petioled up to 15 mm long, although shorter, and relatively slender; blades pubescent on both surfaces, but never pilose or velvety; leaf margins crenate- serrulate; KY-TN-GA-AL-SC ____ **S. nuttallii**

13. Calyx lobes deltoid; flowers 8 or more per verticil; leaf margins crenate-crenulate.

15. Lower leaf surface densely sessile- and stipitate-glandular; blades ovate, widest below the middle; adjacent upper verticils separate in fruit ____ **S. eplingii**

15. Lower leaf surface glandular, but not densely so; blades elliptic-ovate, widest at the middle; adjacent upper verticils commonly crowded in fruit ____ **S. iltisii**

12. Stem sides glabrous, the angles pubescent.

16. Fruiting calyx lobes lanceolate or deltoid-acuminate, more than half as long as the calyx tube.

17. Calyx hispidulous to strongly hispid with long, stiff hairs; stem angles moderately to densely pubescent; leaves subsessile, with very short petioles; bracts abruptly reduced upward from lowest flowering node ____ **S. hispida**

17. Calyx sparsely to moderately pubescent with short soft hairs; stem angles moderately pubescent to nearly glabrous; leaves with petioles 1 to 3 cm long; bracts gradually reduced upward from lowest flowering node ____ **S. subcordata**

16. Fruiting calyx lobes triangular-deltoid and abruptly apiculate, less than half as long as the calyx tube.

18. Stem nodes not bearded (sometimes obscurely fine- hairy); stem angles with scattered, pustulate, short deflexed hairs; plants of high-elevation montane habitats ____ **S. latidens**

18. Stem nodes bearded; lower stem angles copiously pubescent with 3-celled spreading hairs; plants of low-elevation Piedmont and Coastal Plain habitats ____ **S. matthewsii**

KEY 2

1. Fruiting calyx lobes deltoid to broadly triangular, less than half as long as the calyx tube.

2. Stem sides pubescent; foliage glandular, often musky-scented when crushed.

3. Petioles short to absent, blades mostly rounded to truncate-cordate.

4. Lower leaf surface densely glandular with atomiferous/short- stipitate golden glands; blades generally ovate, broadest toward the base ____ **S. eplingii**

4. Lower leaf surface glandular, but not densely so; blades generally elliptic, somewhat lyrate toward base, broadest near the middle ____ **S. iltisii**

3. Petioles well developed, blades cordate at base.

5. Top of blooming stem frequently flexuous, somewhat lax; blades ovate-rounded ____ **S. cordata**

5. Top of blooming stem stiffish, not lax; blades oblong-elliptic ____ **S. nuttallii**

2. Stem sides glabrous; foliage not glandular (occasionally with a few scattered glands) or musky-scented.

6. Stem nodes not bearded (sometimes obscurely fine-hairy); stem angles with scattered, pustulate, short deflexed hairs; plants of high-elevation montane habitats ____ **S. latidens**

6. Stem nodes bearded; lower stem angles copiously pubescent with 3-celled spreading hairs; plants of low-elevation Piedmont and Coastal Plain habitats ____ **S. matthewsii**

1. Fruiting calxy lobes lanceolate, narrowly triangular, deltoid-acuminate, or nearly subulate, more than half as long as the calyx tube.

7. Leaf blades linear to lanceolate.

8. Leaf blade margins entire to crenate; plants generally glabrous ____ **S. hyssopifolia**

8. Leaf blade margins serrulate with at least a few teeth; plants glabrous or pubescent.

9. Stems strict or sparingly branched; leaves sessile or barely petioled, the blades crenate to serrate with shallow teeth ____ **S. aspera**

9. Stems frequently lax and branched from the upper nodes; leaves obviously petioled, the blades sharply toothed ____ **S. tenuifolia**

7. Leaf blades wider, rounded, oblong to elliptic.

10. Petioles poorly developed or absent, < ⅕ as long as the blade.
  11. Upper stem sides glabrous.
    12. Calyx hispidulous to strongly hispid with long, stiff hairs; stem angles moderately to densely pubescent; leaves subsessile, with very short petioles; bracts abruptly reduced upward from lowest flowering node ____ **S. hispida**
    12. Calyx sparsely to moderately pubescent with short soft hairs; stem angles moderately pubescent to nearly glabrous; leaves with petioles 1 to 3 cm long; bracts gradually reduced upward from lowest flowering node ____ **S. subcordata**
  11. Upper stem sides variously pubescent or glandular-pubescent.
    13. Corollas purple; rare adventive ____ **S. palustris**
    13. Corollas pink; native species.
      14. Blades copiously pubescent, usually velvety; VA and WV only ____ **S. arenicola**
      14. Blades pubescent but never velvety; KY-TN-GA-AL-SC ____ **S. nuttallii**
10. Petioles obvious, those of the mid stem > ⅕ the length of the blade.
  15. Leaf blades dentate or sharply dentate; stem angles abundantly pubescent with long (to 3 mm), spreading or somewhat retrorse hairs ____ **S. clingmanii**
  15. Leaf margins crenate to serrulate, but never dentate; stem angles glabrous or pubescent (if the latter, then with scattered, stiffish, retrorse hairs).
    16. Annual; corolla scarcely exserted from calyx ____ **S. agraria**
    16. Perennial; corolla prominently exserted from calyx.
      17. Plants commonly glandular on stems, leaves, and within inflorescence.
        18. Rhizomes terminated by white, rounded tubers; blades oblong; weedy ____ **S. floridana**
        18. Rhizomes without tubers; blades elliptic, cordate; not weedy ____ **S. nuttallii**
      17. Plants not glandular on stems, leaves, or within inflorescence.
        19. Calyx usually hispidulous to hispid with stiff, eglandular hairs; fruiting calyx lobes straight and conspicuously apiculate ____ **S. hispida**
        19. Calyx usually glabrous or sparingly pubescent; fruiting calyx lobes usually recurved and only weakly apiculate ____ **S. tenuifolia**

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POLEMONIUM VILLOSISSIMUM (POLEMONIACEAE), AN OVERLOOKED SPECIES IN ALASKA AND YUKON TERRITORY

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ABSTRACT

A new species of *Polemonium*, **P. villosissimum,** is described from the mountains of southern and south-central Alaska and southwestern Yukon Territory. The new species connects to the circumpolar *P. boreale* morphologically, is probably most closely related to that species, but differs in several unrelated characters without any transitional forms having been observed.

RESUMEN

Se describe una especie nueva de *Polemonium*, **P. villosissimum,** de las montañas del sur y sur-centro de Alaska y suroeste del territorio de Yukon. La nueva especies conecta morfológicamente con el circumpolar *P. boreale*, y es probablemente el pariente más cercano de esa especie, pero difiere en varios caracteres no relacionados sin que se haya observado ninguna forma de transición.

The genus *Polemonium* L. (Polemoniaceae) is predominantly western North American but has several representatives in eastern North America, Europe, and Asia. One of the most widespread and also polymorphic species is *P. boreale* Adams, described from the mouth of Lena River in northern Siberia, but with a circumpolar distribution in the Arctic and extensions southwards into northern boreal mountains. Hultén (1948) stated that he had worked with Davidson on his material and that they were unable to find characters for subdividing *P. boreale*. Accordingly, in his monograph of the genus, Davidson (1950) treated the species collectively.

However, years later, Hultén (1967) formalized variation in Alaska as 1) subsp. *boreale* (implied), 2) subsp. *macranthum* (Cham.) Hultén, based on *P. humile macranthum* of Chamisso (1831), described from St. Paul Island and reported by Hultén from "along the southern coast of western Alaska," and 3) var. *villosissimum* Hultén, based on a collection from Cathedral Mountain, Denali National Park, in the Alaska Range (HOLOTYPE: S!; ISOTYPE: ALA!). Whereas Hultén (1968) mapped subsp. *macranthum* with a range in southwestern Alaska, he merely mentioned var. *villosissimum* in passing as a plant of the high mountains of central and southern Alaska. His diagnosis of var. *villosissimum* is brief: "Inflorescentia dense capitata longe albo-villosa."

The tall-growing and large-flowered plants Hultén assigned to subsp. *macranthum* represent an endpoint of continuous variation within *P. boreale* and do not, in our view, merit taxonomic recognition. Variety *villosissimum* is another matter. This taxon is now documented at ALA from more than 35 sites from the St. Elias Mountains of southwestern Yukon throughout the Alaska Range and the more southern mountains westwards to the Alaska Peninsula and the Kilbuck-Kuskokwim mountains (Fig. 1). These specimens show several differentiating characters in addition to the two emphasized by Hultén. Variety *villosissimum* is for the most part sympatric with *P. boreale* in central and southern Alaska, but it is generally found at higher elevations and in screes, often irrigated by meltwater from snowbanks. None of the specimens of var. *villosissimum* show features transitional to *P. boreale*; thus, we conclude that Hultén's var. *villosissimum* represents a fully independent species and hereby combine it as such with an emended description.

Polemonium villosissimum (Hultén) D.F. Murray & Elven, comb. et stat. nov. (**Figs. 2, 3**). BASIONYM: *Polemonium boreale* Adams var. *villosissimum* Hultén, Ark. Bot. 7:113. 1967. TYPE: ALASKA: McKinley Park, Cathedral Mt, Jul 1964, *E. Hultén & A. Murie* (HOLOTYPE: S!; ISOTYPE: ALA!).

Perennial, with a prolonged, distally richly branched root-stock typical of scree plants; 5–20 cm tall; stems

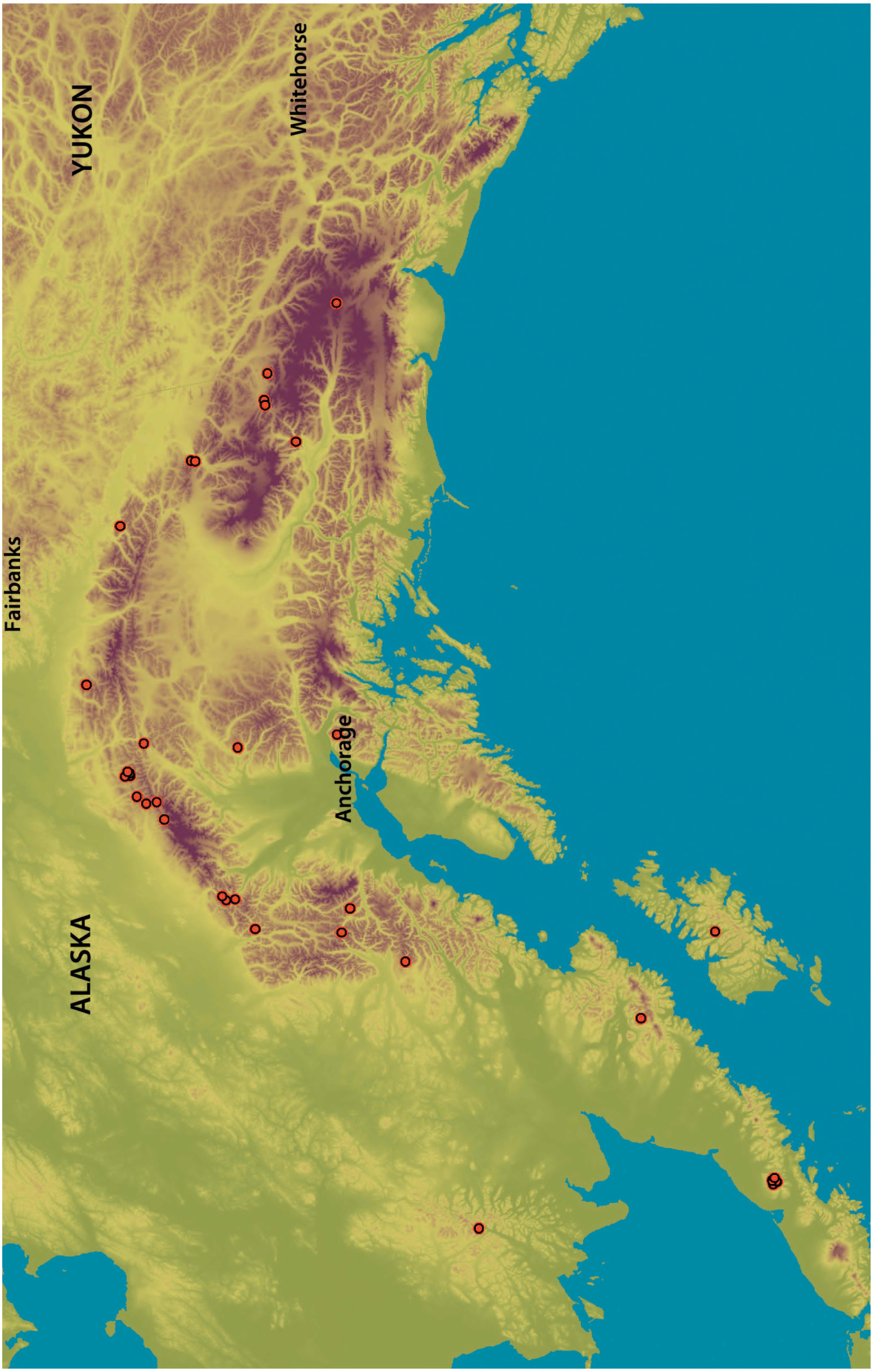

Fig. 1. Range of *Polemonium villosissimum* based on specimens at ALA.

Fig. 2. ***Polemonium villosissimum*** **(Hultén) D.F.Murray & Elven. Voucher: Canada. Yukon. Mount St. Elias Quad.: Outpost Mt. S end Kluane Lake, ca. 2140 m, 60 65'N, 138 22'W, 22 Jul 1969,** ***D.F. Murray 3015*** **(ALA). Photo: D.F. Murray.**

solitary to several, erect or suberect from dense cluster of basal leaves; basal leaves 2–8 cm, with (9–) 11–21(–23) obliquely ovate to obovate leaflets, apices rounded to obtuse, 4–10 × 3–8 mm, decurrent and confluent with distinct rachis wings, villous; stem leaves 2–3, similar to basal leaves; inflorescence strongly congested, 5–10 flowers or more, compact and head-like until maturation of the fruits; pedicels, bracts and calyces long-villous, eglandular; pedicels less than half the length of the calyx, 3–7 mm; proximal bracts foliar, distally absent; calyx 7–10 mm, campanulate, segments equalling or slightly shorter than the tube, narrowly triangular–ovate, apices obtuse or rounded; corolla narrowly campanulate, 10–15 mm long, 5–10

Fig. 3. ***Polemonium boreale*** **Adams. Voucher: USA. Alaska. Harrison Bay Quad.: National Petroleum Reserve-Alaska. Vic. Fish Creek test well 1, ca. 30 m. 70 19'N, 151 58'W, 27 Jul 1977,** ***D.F. Murray & A.W. Johnson 6619*** **(ALA). Photo: D.F. Murray.**

mm broad, lobes narrowly obovate to broadly linear, 7–11 × 3–6 mm, longer than the tube, cream to purplish blue, often blue proximally and cream distally; stamens shorter than the corolla; style very short, stigmas inserted well below the stamens, anthers yellow; flowers with sweet fragrance.

We have examined specimens of *P. boreale* from arctic Europe, Siberia, Canada, Greenland, Alaska and Yukon and found none that approached *P. villosissimum*. Diagnostic characters between these two species are given in Table 1 and several of these features are evident in Figures 2–3.

Table 1. Characters differentiating *Polemonium villosissimum* from *P. boreale.*

	P. villosissimum	***P. boreale***
Leaflets	thickened	not thickened
Inflorescence	capitate	open
Flowers	5–10(–15)	1–5
Eglandular hairs	densely villous	sparsely to densely villous
Glandular hairs	absent	dense
Calyx lobes	narrowly ovate	ovate
Corolla shape	narrowly campanulate to funnelform	broadly campanulate to rotate
Corolla color	cream, purplish blue	uniformly blue or bicolorous
Corolla lobe	narrowly obovate or broadly linear	broadly obovate as broad as long
Stigma vs anthers	short, well below anthers	long, equalling or well above anthers
Anthers	yellow	white
Fragrance	strong (absent from Kodiak populations)	absent

Polemonium villosissimum is a specialist of mobile high alpine screes and exposed ridges, mainly on calcareous or circumneutral substrates, mostly found at much higher elevations than the largely sympatric but mainly arctic *P. boreale*. One low-elevation site is at the Aniakchak Caldera of the Alaska Peninsula (reported at 325 m a.s.l.), but the majority are from above 1000–1500 m, which is alpine at this northern latitude. The highest records are from above 2500 m in the St. Elias Mountains.

We have examined specimens from four localities where *P. boreale* occurs in the same area with *P. villosissimum* (vic. Rusty Glacier, Outpost Mountain, vic. Russell and Guerin glaciers) in the central and northern St. Elias Mountains. No transitional specimens between the two species were found at these localities.

Polemonium villossisimum in the St. Elias Mountains is generally found above the limits of glacial ice during the last glacial maximum, hence nunatak persistence is postulated. Since *P. boreale* typically occurs at lower elevations, we presume the species would have been extirpated by the glaciers. Hence, the two species must have been well isolated from each other for a long period of time. Recolonization of *P. boreale* likely came from the unglaciated areas in central Yukon or from Alaska.

The species is diploid with $2n = 18$ (Dawe & Murray 1979, the chromosome count based on material from the type locality, Cathedral Mt).

Specimens seen: **U.S.A. ALASKA:** Base of Knife Peak Volcano, Valley of 10,000 Smokes, Katmai N.M., pumicious sand, 7 Aug 1954, *P. Schaller* (ALA); 2 mi S Kukak Volcano, Katmai N. M., 26 Jul 1953, *Williams & Cahalane 354* (US); Denali N.P.: top of McGonnigal Pass, ca. 7,000 ft, 1 Aug 1939, *A. Nelson & R.A. Nelson* (ALA); Alaska Peninsula: Aniakchak N.M., Aniakchak Caldera, cone 1445, cinder cone slope with scattered alpine herbs, 1250 ft, 1993, *L. Hasselbach s.n.* (ALA); Denali N.P.: Sable Mt., 2 Aug 1959, *L. Chene 371* (ALA); Chugach State Park: Eklutna Valley, Twin Peaks Trail Ridge, 1200–1400 m.s.m, exposed SSW slope, sparsely vegetated rock fragments, Valdez Group, 21 Aug 1984, *L. Marvin 1869* (ALA); headwaters Mazuma Creek, E of Chickaloon, 6500–7000 ft, 17 Jul 1922, *R.A. Pope s.n.* (S); Copper R. region, 5500 ft, 1902, *W.L. Poto 27* (S, US); McCarthy Quad.: vic. of the Guerin Glacier terminus, upper White R. valley, in deposits of volcanic ash, 3 Aug 1968, *D.F. Murray 2026* (ALA); McCarthy Quad.: vic. of the Guerin Glacier terminus, upper White R. valley, N-facing scree, 4 Aug 1968, *D.F. Murray 2097* (ALA); McCarthy Quad.: vic. Sheep Glacier terminus, upper White River valley, 15 Aug 1968; *D.F. Murray 2256* (ALA); McCarthy Quad.: vic. Russell Glacier terminus, upper White R. valley, high elevation scree, 11 Aug 1968, *D.F. Murray 2191* (ALA); McCarthy Quad: Wrangell Mts, vic. plateau W of Nizina R., above head of Nikolai Cr., 1520 m, SE-facing shaly scree near ridge crest, 24 Jul 1996, *A.R. Batten & M.H. Baker 96-67* (ALA); Nabesna Quad: Mentasta Mts, vic. Nabesna R. valley, growing in unstable scree in alpine glacial bowl area, 26 Jul 1996, *V. Moran 84* (ALA); Nabesna Quad: Mentasta Mts, vic. Nabesna R. valley, alpine glacial bowl and outwash area, 25 Jul 1996, *V. Moran 51* (ALA); Tanacross Quad.: Sheep Creek, talus, S-facing slope, 1645 m, 20 Jun 1978, *J. Winters Jr. 347* (ALA); Alaska Range: Dry Creek, 4,800 ft, scattered on rocky, Dryas, S-facing slope, 27 Jun 1962, *L.A. Viereck & K. Jones s.n.* (ALA); do Aug-Sep 1962, *L.A. Viereck s.n.* (S); Cantwell, 10 Jul 1927, *L. J. Palmer 1910* (ALA, US, S); Talkeetna Mts Quad.: Wells Mt. area, alpine rock slope mixed with herbaceous tundra, 17 Jul 1979, *E. Helmstetter 117-19* (ALA); Healy Quad.: Cathedral Mountain, alpine,1–10 Jul 1964, *A. Murie & E. Hultén s.n.* (ALA); Denali N.P.: Park Highway Mile 36. Cathedral Mountain,1–10 Jul 1964, *E. Hulté s.n. [& A. Murie]*(S); Cathedral Mt., 6 Aug 1939, *F. A. Warren W-2143* (US); Healy Quad.: Denali N.P., Igloo Mt., 13 Jun 1941, *A. Murie* (ALA); Healy Quad.: Cathedral Mt, steep alpine screes and ridge crest outcrops, 1220 msm [$2n = 18$, J.C. Dawe 1980], 18 Aug 1976, *D.F. Murray 6239* (ALA); Healy Quad.: Denali N.P., Igloo Mt., 13 Jun 1941, *A. Murie* (ALA); Mt. McKinley Quad.: high point of ridge between

Toklat and Bergh Lake, amongst rubble near peak top, 1841 m (top of peak 1885 m), 22 Jun 1979, *S. Carwile 79-119* (ALA); Denali N.P.: jct. Muldrow Glacier and the glacier from Anderson Pass, early pioneer on the lateral moraine of the Muldrow, 4,000–5,000 ft, 17 Jul 1956, *L.A. Viereck 1391*(ALA); Denali N.P.: NW slope to summit of Mt. Eielson (Copper Mt.), 5,800 ft, talus slope on the summit ridge, 25 Jul 1956, *L.A. Viereck 1506* (ALA, COLO, S); Alaska Range Distr.: upper valley of the Swift Fork of the East Fork of the Kuskokwim R., on exposed ridge top, 5,000–5,700 ft, 15 Jul 1961, *L.A. Viereck 5011* (ALA); Alaska Range Distr.: upper valley of the Swift Fork of the East Fork of the Kuskokwim R., on exposed ridge top, 5,000–5,700 ft, 26 Jul 1961, *L.A. Viereck 5162* (ALA); Talkeetna Quad.: Denali N.P., limestone outcrops on W bank of W Fork Yentna R., 1.7 km NW of confluence of W Fork Yentna with stream draining Shadows Glacier, S facing scree, 1067 m, 1 Aug 2001, *A. Larsen & A. Batten 01-0821* (ALA); Talkeetna Quad.: Denali N.P.: W side of canyon in headwaters of W Fork of Yentna R., 4 km SW of Mystic Pass, in rubble and scree on SE-facing slope, 1128 m, 27 Jun 2000, *C. Roland & A. Batten 4308* (ALA); Tyonek Quad.: Alaska Range, ridge S Max Lake, 1442 m, 13 Jul 2002, *A. R. Batten & M. H. Barker 02-394* (ALA); McGrath Quad.: Teocalli Mts, Lynx Creek drainage, mixed calcareous sandstone-shale-siltstone screes and ridgetops, 1380–1740 m, 2 Jul 1983, *C. Parker 810* (ALA); Lime Hills Quad.: Lake Clark N.P.P., Alaska Range, headwaters of Chilligan R., S trending ridge above S side of Chilligan R., 1554–1707 m.s.m, fines, small scree, mixed igneous & carbonate substrates, 23 Jun 2001, *R. Lipkin & A. Jansen 01-20* (ALA); Kodiak Quad.: Kodiak I., vic.Uganik Lake, ca 8 km SSW of lake, small cirque basins at headwaters of South Arm of Uganik Bay, loose S-facing scree, 800–975 m, 28 Jul 2006, *C. L. Parker & S. Studebaker 16735* (ALA); Lake Clarke Quad.: Neacola Mts, Turquise Lake, W end, 10 Jun 1996, *P. Caswell 96426* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Amiakchak Crater, W side of Surprise Lake, S of Bolshoi Dome, 335 m, 13 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-238* (ALA); Chignik Quad.: Surprise Lake, Aniakchak Caldera, unstable cinder slope, 12 Jul 1987, *Bosworth & Koren* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Aniakchak Crater, SW side of Surprise Lake, 351 m, 14 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-244* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Aniakchak Crater, ridge NE of Vent Mt, 475 m, 17 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-265* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Aniakchak Crater, lava dome at NW end of Surprise Lake, NW of Bolshoi Dome, 366 m, 18 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-240* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Aniakchak Crate, E slope Vent Mt, 733 m, tephra slope, 17 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-267* (ALA); Chignak Quad.: Alaska Peninsula, Aleutian Range, Aniakchak Crater, NE of 1931 vent, 442 m, 12 Jul 2004, *R. Lipkin, M. Duffy, K. Bosworth & A. Miller 04-230* (ALA); Goodnews Quad.:Kilbuck-Kuskokwim Mts, High Lake, 14 mi N Togiak Lake, boulder field in cirque, 25 Jul 1995, *P. Caswell 368-95* (ALA).

CANADA. YUKON TERRITORY: St. Elias Mts.: mt. adj. Kaskawulsh Glacier vic. jct. north arm, Jul 1965, *Anderton & Freeman s.n.*(ALA); St. Elias Mts.: Steele Glacier and vic., dry coarse soil on ridge crest, 7,000 ft, 05–10 Aug 1967, *D.F. Murray & B.M. Murray 1367* (ALA, CAN); Kluane N.P.: Hoge Mt. E slope, ca. 12 mi SW of Burwash Landing, alpine talus slope, ca. 6,500 ft, 11 Aug 1974, *G.W. Douglas & G. C. Douglas 7879* (ALA); Mount St. Elias Quad.: Outpost Mt. S end of Kluane Lake, ca. 2140 m, 22 Jul 1969, *D.F. Murray 3015* (ALA); St. Elias Mts, upper Hubbard Glacier nunatak, 7,500–7,900 ft, SW-facing granite rock, 8 Aug 1966, *V. Hoeman s.n.* (ALA); Mount St. Elias Quad.: nunataks vic. of upper Seward Glacier, 1800–2140 m, 18 Jul 1971, *D.F. Murray 3432* (ALA); Mount St. Elias Quad.: nunataks vic. upper Seward Glacier, 1800–2140 m.s.m, 19 Jul 1971, *D.F. Murray 3465* (ALA); Kluane Lake Quad.: vic. Rusty Glacier terminus, W of Burwash Landing, 15 Jul 1968, *D.F. Murray s.n.* (ALA); Kluane Lake Quad.: vic. of Rusty Glacier terminus, W of Burwash Landing, 11 Jul 1968, *D.F. Murray 1718* (ALA).

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A NEW VARIETY OF *HOLODISCUS DUMOSUS* (ROSACEAE: SPIRAEOIDEAE) FROM COASTAL NORTHWESTERN CALIFORNIA

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ABSTRACT

Holodiscus dumosus var. **cedrorus** is proposed for a localized endemic confined to The Cedars area of Sonoma Co., California. The new variety differs from *H. dumosus* var. *glabrescens* by being a taller shrub with sparser, more open branches, inflorescences composed of numerous secondary branches subtended by bracts, panicles of 70 or more flowers, and achenes with more than 35 glands per side. The new vegetative growth is consistently, and distinctively, a bright ruby red in color. The new variety is a serpentine endemic confined to the outer Coast Ranges of California.

RESUMEN

Se propone **Holodiscus dumosus** var. **cedrorus** para un endemismo confinado al área de The Cedars de Sonoma Co., California. La nueva variedad difiere de *H. dumosus* var. *glabrescens* por ser un arbusto más alto con ramas separadas más abiertas, inflorescencias compuestas de numerosas ramas secundarias subtendidas por brácteas, panículas de 70 o más flores, y aquenios con más de 35 glándulas en cada lado. El crecimiento vegetativo nuevo es consistentemente, y distintivo, de un color rubí brillante. La nueva variedad es un endemismo de las serpentinas confinado a la Cordillera Costera de California.

The Cedars of northwestern California comprises about 6,000 acres of ultramafic (high magnesium and iron) rock and derived soils located in Sonoma Co. These rocks are commonly referred to as serpentine. Serpentine has a profound effect on vegetation due to an imbalance of magnesium to calcium, and a lack of essential nutrients for plant growth. Geophysical isolation of The Cedars from other serpentine areas, dramatic topographic relief, high winter rainfall and unusually hot summer temperatures, are factors that have fostered an exceptionally high level of endemic taxa on this geologic "island." They are: *Arctostaphylos bakeri* Eastw. ssp. *sublaevis* P.V. Wells, *Calochortus raichei* Farwig & Girard, *Epipactis gigantea* Hook. f. *rubrifolia* P.M. Br., *Erigeron serpentinus* G.L. Nesom, *Eriogonoum cedrorum* Reveal & Raiche and *Streptanthus glandulosus* Hook. ssp. *hoffmanii* (Kruckeb.) M.S. Mayer & D.W. Taylor. In addition to the endemic taxa, many others are disjunct or represent a range extreme at The Cedars.

The Cedars *Holodiscus* was first noted by Raiche in 1981 who introduced the plant into the University of California Botanical Garden at Berkeley in 1982 where it has persisted in cultivation ever since. He noted that the plant differed significantly from the common coastal oceanspray, *H. discolor* (Pursh) Maxim, which occurs less than a mile away on non-serpentine substrate. Using the most recently published monograph by Ley (1943), he attempted to ascertain in this complex genus of eight species where this particular expression fit best. He initially sought to fit The Cedars plant into one of the published expressions of *H. discolor* only to conclude that it persistently tended to key out to what Ley termed *H. microphyllus* Rydb. and specifically the var. *glabrescens* (Greenm.) Ley, a plant found in the Sierra Nevada and mountains of central and eastern Oregon eastward to Wyoming, Utah and northwestern Arizona, well away from The Cedars, a mere seven air miles east of the Pacific Ocean in Sonoma Co., California.

By studying the plant over the years, and growing the plant in several different locations, noting that it retained its consistent features, Raiche concluded that the plant was distinct and required formal recognition. Working with Reveal while they jointly examined another local endemic, *Eriogonum cedrorum* (Reveal & Raiche 2009), they began a detailed study of the two species of *Holodiscus* found in the United States and Canada, and concluded that The Cedars oceanspray is a variant of *H. dumosus*, and that the traditional cir-

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cumscription of species in the genus failed to take into account a series of important features about branches. The branch type is a crucial determinant of leaf morphology, on which so much of *Holodiscus* taxonomy has been based. Thus it is crucial that comparable leaves are being compared in each taxon. Additional details about the small flowers overlooked by previous workers also proved noteworth. In particular, details about the complex stamen arrangement, especially filament size, shape and position on the hypanthium have not been consistently noted for most taxa in the genus. In addition, the number of glands on the face of the achenes provides important data to make distinctions within the genus. The long and detailed description which follows attempts to better describe and quantify those features that future workers need to consider in evaluating the remaining species and varieties of this genus.

Holodiscus dumosus (Nutt. ex Hook.) A. Heller var. **cedrorus** Raiche & Reveal, var. nov. (**Figs. 1–5**). Type: UNITED STATES. California: Sonoma Co.: The Cedars, Central Canyon area NE of Laton [or Layton] Mine, on gravelly, serpentine slopes at 270 m elev., 38°37'16"N, 123°08'00"W, T9N,R12W, sec. 13 SW¼ of the NE¼, 7 Jun 2010, *J.L. Reveal & R. Raiche 8999* (holotype: NY; isotypes: ARIZ, ASU, BH, BM, BRY, CAS, COLO, GH, LL, MICH, MO, OSC, RENO, RM, RSA, TEX, UC, US, UTC, WTU).

A var. *glabrescens* insigniter elatis et plus apertis cum novis caules, ramis et petiolis valde et laete rubineis, et foliis atrovirides superficiaris differt.

Plants long-lived, deciduous woody shrub, 1–2 (–2.5) m tall forming sparse, open thickets, deeply rooted, spreading slowly underground by rhizomes, resprouting after catastrophic loss of above ground parts, each branch living at least 2–3 decades, possibly longer before senescing, continuously replaced by new branches. **Branches** of two types, primary and secondary. **Primary branches** (Fig. 3) strict, up to 3 m long, unbranched or nearly so, 3–5 mm thick, initially ruby red, aging to reddish tan, glabrous or only sparsely pubescent with the hairs often early deciduous; bark thin, papery, with 5-8 ribs, smooth or finely striate between ribs, outer bark splitting in long vertical fissures but remaining on stem during first season, tan to reddish tan, aging to gray, inner bark deep reddish brown (on tall shrubs, sometimes secondary branches appear on primary branches, but resemble primary branches in size, robust growth and leaf characters). **Secondary branches** (Fig. 4) shorter, repeatedly and divaricately branched with the ultimate branchlets often reduced to peg-like spurs 1–2 cm long, 1–3 mm thick, initially ruby red, becoming opaque gray to reddish tan, initially sparsely pubescent with scattered glands, hairs and glands early deciduous; bark similar to that of the primary cane branches. **Leaves** emerging in early spring (Feb/Mar) and often becoming summer deciduous (Aug) in dry years, otherwise not until fall (Oct), variable according the branch type, shiny and dark green to blackish adaxially when exposed to full sun, often appearing whitish due to stomata abaxially, newly emerging petioles and leaf blades suffused with strong red coloration similar to that of stems and branches, this diminishing with age but still noticeable on mature foliage, becoming a soft golden yellow just prior to leaf drop; blades glabrate or sparsely pubescent with fine hairs and scattered glands adaxially, both deciduous with age, short puberulent with a few glands (not readily visible) abaxially especially on young leaves, primary veins sunken on adaxial surface, these finely pubescent with slightly appressed and persistent hairs abaxially. **Primary stem foliage** (Fig. 3) large, internodes 7–43 mm long, blade typically ovate to deltoid-ovate or roundish, 13–43 mm long (incl. 3–17 mm long petiole), 11–35 mm wide, leaf base often slightly decurrent, otherwise flat to broadly angled relative to central leaf rib, lobes 4–5(–6) per side, shallowly toothed extending past midpoint, sometimes lower lobes incised to near midrib and appearing almost pinnate, often with 1–5 secondary teeth especially on larger leaf blades, each apically rounded or mucronate. **Secondary stem foliage** (Fig. 4) small, 5–25% the size of that found on primary stems, often seemingly in fascicles on short shoots; mostly obovate; blade oval or roundish, 6–21 mm long (including 3–4 mm long petiole), 4–13 mm wide, leaf base minutely decurrent up to half the length of the petiole, teeth usually 3–4 per side and restricted to upper half of margin, secondary teeth lacking, each apically minutely mucronate. **Inflorescences** panicles or compound panicles (Fig. 1) at ends of primary, secondary or tertiary branches (not on peg-like branches), positioned above the foliage, largest and densest on primary stems, decreasing with branch size, often suffused with pink coloration with this persisting after flowering, aromatic (*Myrica*-like) when crushed, diffuse, open; branchlets of compound panicles 7–13(–16), these again often

Fig.1. *Holodiscus dumosus* var. *cedrorus.* Flowering panicles. Fully open flowers ± 6 mm across, arranged in compound panicles, the secondary panicle branchlets subtended by leaf-like bracts. All young growth, including inflorescence (including sepals) suffused with red or pink coloration.

Fig. 2. *Holodiscus dumosus* var. *cedrorus*. Close up of flower showing 5 pistils in center, golden nectary ring on hypanthium, 20 stamens, 5 sepals and 5 petals ± 0.2 mm longer than sepals. The 20 filaments are inserted at three slightly different positions on the outer rim of the hypanthium, and reflex at different times depending on their respective positions.

branched, each primary lower branchlet subtended by a small leaf-like basal bract 6–7 mm long and 3.5–4 mm wide at lower nodes, these decreasing in size upward and ultimately lacking. **Flowers** (Fig. 2) numerous but extremely variable in number, 70-700, averaging 200 per terminal panicle; calyx 5, persistent, 1.8–2 mm long, 1.4–1.5 mm wide at base, triangular ovate, pubescent and minutely glandular on both surface but more densely so abaxially; sepals hygroscopic, closing inward when wet and reflexed when dry; hypanthium round-pentagonal in outline with the broadest points between the sepals, 1.7–2 mm across, adnate to ovary, pubescent and glandular within, nectary forming a ring between outer and inner rim; **petals** 5, inserted on outside top of outer rim of hypanthium, oval, tapering to a narrow base, 1.8–2.1 mm long, 0.9–1 mm wide, deciduous. **Stamens** 20, arranged in two series with 5 opposite the petals and 15 opposite the sepals; filaments 1.6–1.9 mm long, arising on the inside of outer hypanthium rim, three filaments on sepals flaring at base and of two lengths with central one positioned on inside of outer hypanthium rim and 1.6 mm long, outer two filaments 1.9–2.1 mm long and inserted on top of outer hypanthium rim, these curved outward initially with those opposite petals and central sepal stamen curving outwardly sequentially. **Pistils** with styles 1–1.1 mm long. **Achenes** 5, radial, arranged opposite the petals, laterally flattened, 2–2.1 mm long, densely pilose with long, stiff hairs marginally, otherwise merely pubescent and persistently glandular with (30–)35–45(–50) prominent, sessile or stalked glands per face (Fig. 5).

Fig. 3. *Holodiscus dumosus* var. *cedrorus*. Primary branch segment showing large foliage type; typically with truncate base, deep lower lobes, the lower lobes frequently with secondary lobing. Minute glands not apparent on foliage without magnification. Branch color in transition from bright red to cinnamon, typical of first year growth.

Fig. 4. *Holodiscus dumosus* var. *cedrorus*. Secondary and tertiary branches with ruby red new growth. Foliage smaller than on primary stems, with cuneate bases, fewer, shallower lobes, usually lacking secondary lobing, leaf base sometimes decurrent along petiole for all or part of length (lower center leaf).

Distribution.—Restricted to serpentine substrates at The Cedars 200–620 m elev, Sonoma Co., California (Fig. 6). May–Jul.

Additional collections examined: **U.S.A. CALIFORNIA. Sonoma Co.:** The Cedars near Big Austin Creek and Layton Mine, 259 m, 20 May 1987, *Raiche 70194* (JEPS); The Cedars, in the canyon above Austin Creek near Layton Mine, on serpentine gravelly slopes at 1350 ft elev., 38°37'16"N, 123°07'37"W, T9N,R12W, sec. 13, 28 Jul 2009, *Reveal & Raiche 8991* (BH, UC).

Our recognition of *Holodiscus dumosus* as distinct from *H. discolor*, following Hitchcock (1961) and Holmgren (1997), rather than merging the two as proposed by Lis (1993) who then recognized *H. microphyllus* at the species rank rather than including this expression within *H. dumosus*, is based on a broad knowledge of these plants in the field and the original type material. The two species recognized here are not known to hybridize and their distinction in the Pacific Northwest, and especially in Idaho, where their ranges overlap—although the populations never intermix—are consistently and easily recognized. Even in California the ranges of *H. discolor* and *H. dumosus* do not overlap geographically, and even when the two are in close proximity, as is the case of the new variety proposed here, they occur in markedly different ecological settings. Contrary to Lis, a more troublesome distinction is between *H. dumosus* and *H. microphyllus*, and so much so in the Intermountain West that Welsh (2003) joined Hitchcock and Holmgren in not recognizing *H. microphyllus*

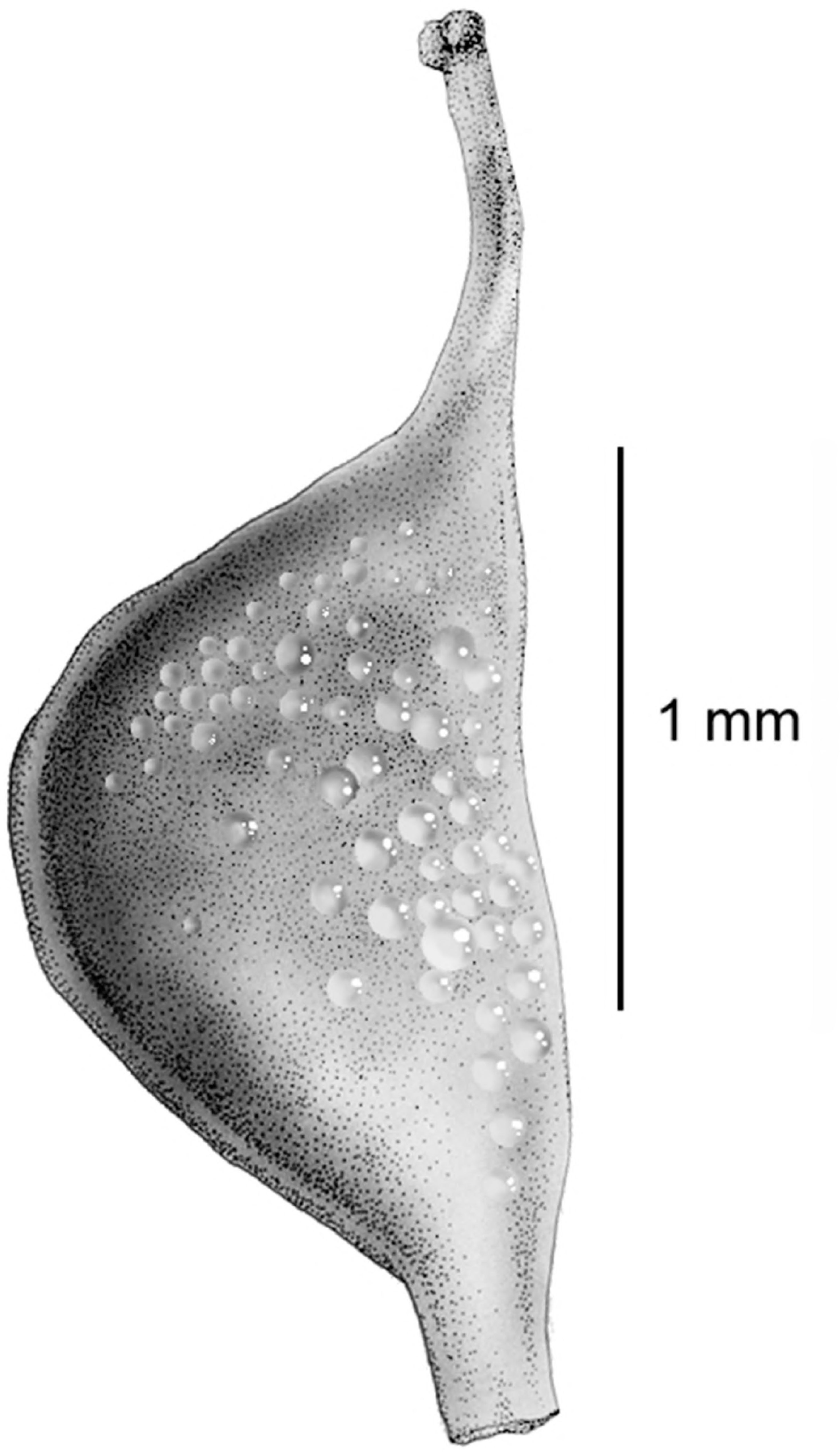

Fig. 5. *Holodiscus dumosus* var. *cedrorus.* An achene showing the variation in size and general distribution of surfaces glands; hairs on the achenes are not shown. Illustration by Alfonso Doucette.

as distinct from var. *dumosus*. Likewise, contrary to what Lis may well propose in a forthcoming volume of *Flora of North America*, a distinction between his *H. microphyllus* var. *microphyllus* and var. *sericeus* F.A. Ley completely breaks down in portions of southern Nevada and southeastern California, and in Arizona any recognition of two entities based on the length of hairs is impossible as this feature is clearly influenced by exposure and elevation where mixed populations of individuals with differences in hair length are the norm.

Thus, here we recognize two morphological and geographically distinct species, *Holodiscus discolor* and *H. dumosus*, while recognizing that a distinction between var. *dumosus*, var. *glabrescens*, and even var. *cedrorus*, is marred by overlaps in some morphological features although var. *cedrorus* is geographically isolated from both.

Holodiscus dumosus var. *cedrorus* (from the Latin *cedrorus*, of cedars) is restricted to ultramafic substrates (peridotite and serpentinite) that defines The Cedars. The plant is fairly common on the lower canyons slopes in relatively mesic, old-growth *Hesperocyparis sargentii* (Jeps.) Bartel woodland where it may be encountered even in dense shade. This is often the only shrub of open talus slopes and is sometimes found in chaparral, particularly on slopes with a north aspect. In general, the variety is associated with *Quercus durata* Jeps., *Umbellularia californica* (Hook. & Arn.) Nutt., *Arctostaphylos viscida* Parry ssp. *pulchella* (Howell) P.V. Wells, *A. bakeri* ssp. *sublaevis*, *Rhamnus ilicifolia* Kellogg, *Frangula californica* (Eschsch) A. Gray ssp. *tomentella* (Benth.) Kartesz & Gandhi, *Iris macrosiphon* Torr., *Carex brevicaulis* Mack., *Silene californica* Durand, *Polygala califor-*

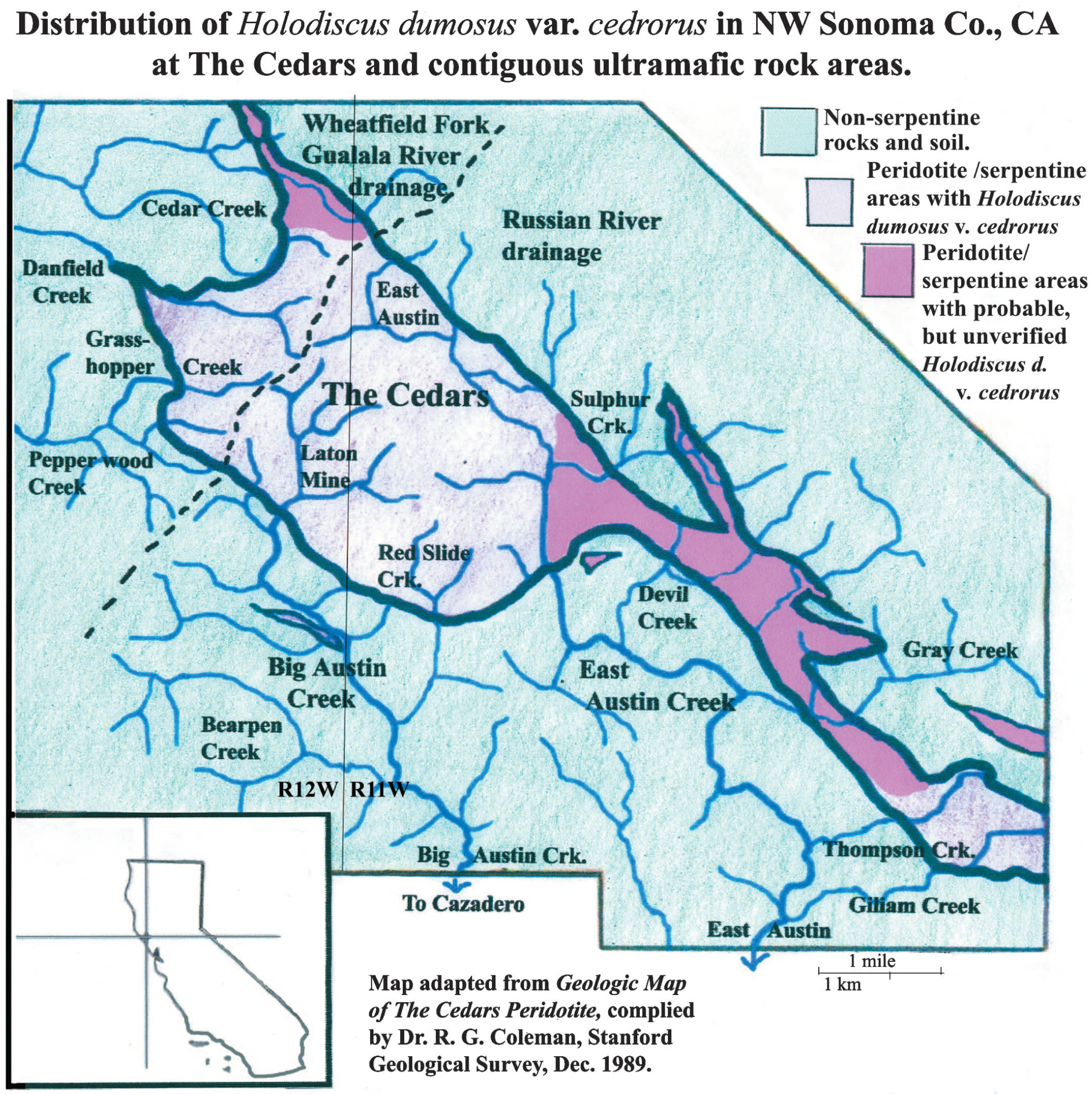

Fig. 6. Map of ultramafic (serpentine) occurrences in the upper drainages of Big and East Austin creeks, and Pepperwood, Grasshopper, Danfield, and Cedar creeks in the Wheatfield Fork of the Gualala River watershed. The occurrence of var. *cedrorus*, where documented, precisely matches the substrate.

nica Nutt. ex Torr. & A. Gray, *Calochortus raichei*, *Erigeron serpentinus, Melica torreyana* Scribn., *Monardella viridis* Jeps., etc. On talus slopes the var. *cedrorus* is associated with *Eriogonum cedrorum*, *E. nudum* Douglas ex Benth. var. *auriculatum* (Benth.) J.P. Tracy ex Jeps., *E. luteolum* Greene, *Streptanthus morrisonii* F.W. Hoffm., *Phacelia corymbosa* Jeps., *Cardamine* aff. *californica* (Nutt.) Greene, *Claytonia exigua* Torr. & A. Gray, *Epilobium minutum* Lindl. ex Lehm., and *Allium falcifolium* Hook. & Arn.

The Cedars *Holodiscus* is clearly allied to var. *glabrescens*. As here defined, in western North America *Holodiscus dumosus* is composed of var. *dumosus* (including var. *australis* (A. Heller) Ley) of western Nevada eastward to Wyoming and south to trans-Pecos Texas and Chihuahua, Mexico, and (as the phase with longer hairs on the leaves termed *Holodiscus microphyllus* var. *sericeus* by Ley) south through southern Nevada, northwestern Arizona, southeastern California to northern Baja California, Mexico. From var. *glabrescens*, var. *cedrorus* may be distinguished by its taller and more open habit (being 1 m or more tall vs. plants mostly

less than 1 m tall) with a more open inflorescence consisting of about twice as many flowers as var. *glabrescens*. The differences in substrate (serpentine vs. volcanic for var. *glabrescens*) is significant although a few populations of var. *glabrescens* are known to occur on serpentine. The abundance of foliar hairs and glands is greater in var. *glabrescens*, and the leaf blades of var. *cedrorus* tend to be more consistently roundish. In var. *cedrorus* the number of glands on an achene is generally more than 35 (Fig. 5) on each face whereas in var. *glabrescens* the number of glands is usually less than 35; there are even fewer achene glands in *H. discolor*. Two features are striking. In var. *cedrorus* the bright ruby red coloration of the young stems, branches and petioles is so obvious that this alone makes the variety an attractive addition to the horticultural trade; in var. *glabrescens* the color is at best a dull red. Added to this are the bright, shiny, dark green to nearly blackish upper leaf surfaces of var. *cedrorus* when exposed to bright light; in var. *glabrescens* the upper leaf surfaces tend to be merely light green or even grayish. Finally, the upper leaf surfaces of var. *cedrorus* are far more consistently glabrous than in most populations of *H. dumosus* var. *glabrescens*.

In summary there is no strong, consistent morphological difference between var. *cedrorus* and var. *glabrescens*, but when combined with the prevailing substrate difference and ecological preference (low elevation vs. montane), there is good suite of characters that makes this entity stand apart. Further, the profound geographic isolation of var. *cedrorus* strongly reinforces even these minor differences. In particular, the bright, ruby red of the stems, branches and petioles is the most obvious and readily observable feature. What might be the significance of this feature is unknown.

The Cedars *Holodiscus*, while common at The Cedars, is the rarest and most restricted entity within the genus. A rough estimate of the number of plants at The Cedars is about 5000. The population is exceedingly stable; during surveys over the last decade of the canyons at The Cedars, not a single dead plant was observed. Some seedlings and juvenile plants were noted, but they are rare. More field work is necessary in the northeastern creeks feeding into East Austin Creek to fully document the range and numbers.

ACKNOWLEDGMENTS

We wish to thank our reviewers, Barbara Ertter and Robert F. Thorne, and as always to patience and understanding the editor extended to us and no doubt others as well over the years he has labored for the benefit of us all. The beautiful achene illustration was done by Alfonso Doucette of Cornell University to whom we are most grateful.

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CYMOPTERUS SPELLENBERGII (APIACEAE), A NEW SPECIES FROM NORTH CENTRAL NEW MEXICO, U.S.A.

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ABSTRACT

Cymopterus spellenbergii is described as new. It has two centers of distribution on the Taos Plateau, New Mexico. Based on morphological and molecular data it is allied with *Harbouria trachypleura*, *Cymopterus bakeri*, *C. filifolius*, and *C. longiradiatus*, all of which occur in New Mexico.

RESUMEN

Se describe como nuevo **Cymopterus spellenbergii.** Tiene dos centros de distribution en la meseta Taos, Nuevo México. Según datos morfologicos y moleculares está relacionado con *Harbouria trachypleura*, *Cymopterus bakeri*, *C. filifolius*, y *C. longiradiatus*, todos ellos presentes en Nuevo México.

More than three decades ago, Richard Spellenberg of New Mexico State University sent the senior author a specimen of umbel from north central New Mexico. He was aware of my interest in western North American members of the family and was curious if it was a novelty.

Initially I assigned it to *Aletes sessiliflorus* W.L. Theob. & C.C. Tseng, although I knew little regarding that taxon, as to my knowledge it had been documented only from the type locality 20 miles west of Cuba, New Mexico (Theobald et al. 1964). Subsequently, I have collected numerous specimens of *A. sessiliflorus* and have studied the holdings of regional herbaria. Published concurrently with *A. sessiliflorus* was *Aletes macdougalii* J.M. Coult. & Rose subsp. *breviradiatus* W.L. Theob. & C.C.Tseng. At that time the subspecies was known only from Montezuma County, Colorado, and adjacent San Juan County, Utah. In recent years several botanists have accumulated numerous specimens of the two taxa from the northwestern quarter of New Mexico and adjacent Arizona, Colorado, and Utah that bridged the morphological gap. This is most apparent with regards to leaf size and shape but it is equally true for other characters provided in the comparison chart by Theobald et al. (1964, p. 311). In general, it appears that as one moves west from the type locality of *A. sessiliflorus*, there is a decline in leaf size, likely due to increased aridity. There are numerous exceptions to this gradient, possibly based on local environmental conditions. Both taxa have terete fruit with membranous wings, unlike the illustrations in the above mentioned paper. Consequently, *A. macdougalii* subsp. *breviradiatus* was elevated to species rank and transferred to *Cymopterus* (*C. breviradiatus* (W.L. Theob. & C.C. Tseng) R.L. Hartm.). It was later placed in synonymy under *Cymopterus sessiliflorus* (W.L. Theob. & C.C. Tseng) R.L. Hartm. (see discussion, Hartman 2006; Goodrich & Hartman, in press).

Returning to Spellenberg's specimen, first collected on Black Mesa just to the west of the Rio Grande and about 17 air miles north-northeast of Española. The taxon that it represents is distinct from *Cymopterus sessiliflorus* in leaf and fruit characters. Furthermore, the taxa are distantly related evolutionarily based on molecular and combined molecular and morphological studies (see below).

Cymopterus spellenbergii R.L. Hartm. & J.E. Larson, sp. nov. (**Fig. 1**). Type: U.S.A. NEW MEXICO: Rio Arriba Co.: 1 mi N of Embudo on the N end of Black Mesa on N facing pocket, T23N, R9E, sec. 14 SW⅛, 15 SE⅛, ca. 6,900 ft, slope 30 percent, pinyon and juniper, sandy soil overlain by basalt rubble, with *Artemisia tridentata, Stipa neomexicana, Sitanion hystrix, Hymenoxys richardsonii,* and *Astragalus puniceus*, 30 May 1984, fruit, *R. & M. Spellenberg, N. Zucker 7753* (holotype: RM; isotype: NMC).

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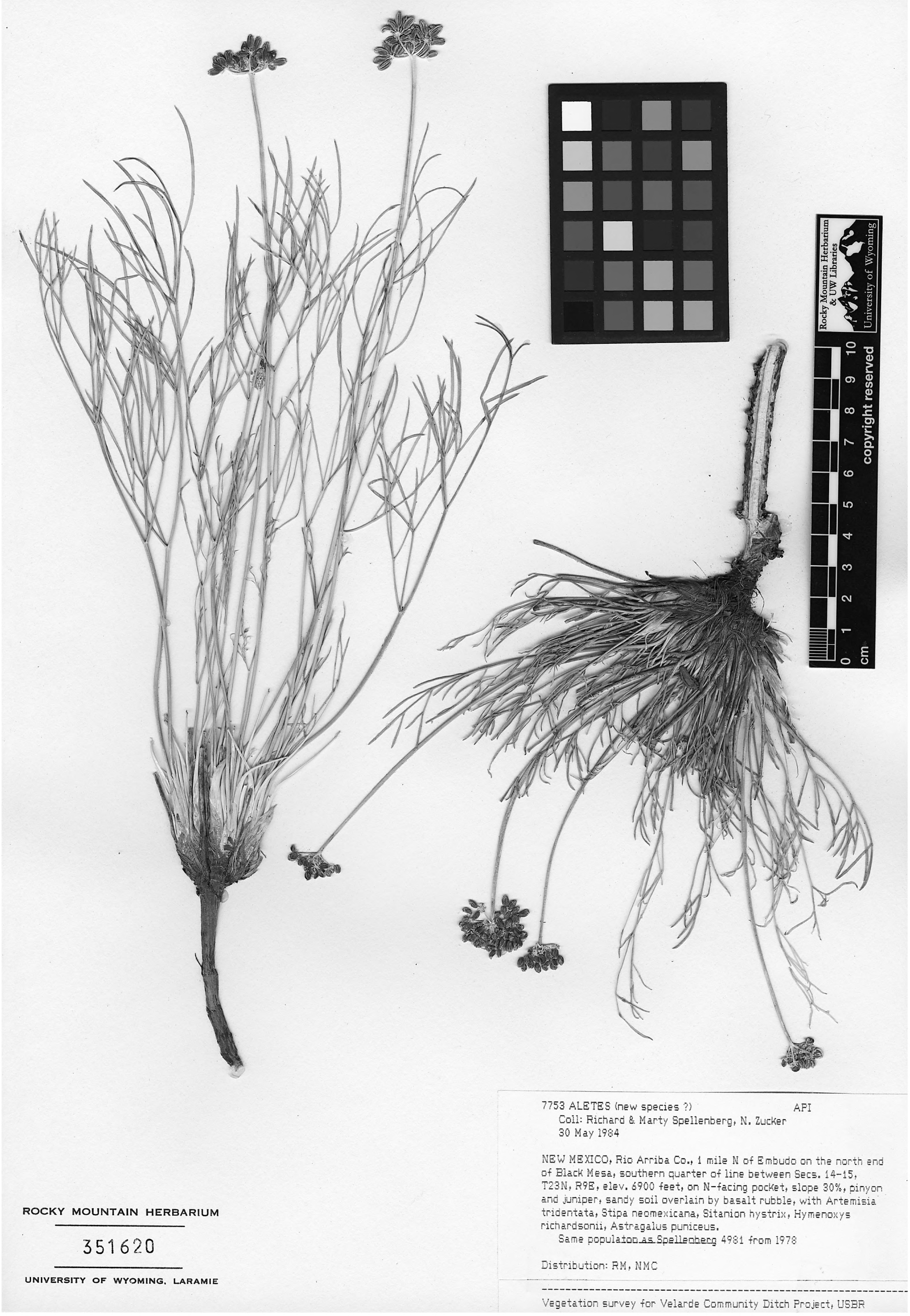

Fig. 1. Photograph of the type specimen, *R. & M. Spellenberg, N. Zucker 7753* (RM) of *Cymopterus spellenbergii*.

Herbae perennes acaulescentes; folia glabra, laminis lanceolatis vel late ovatis 1-pinnatis vel 2-pinnatis foliolis 1 vel persaepe 2 vel 3, sessilibus filiformibus vel linearibus apicibus spinulosis cartilagineis; inflorescentia ex umbellis compositis subcompactis, pedunculis (caulex) 1–5(–11+) simplicis, apices puberuli (25×); involucrum deficiens, radii 6–24; involucellum dimidiatum, bracteolis 5–7 linearibus distinctis; flores flavi, sepalis chartaceis deltoideis vel oblongis vel obsoletis, petalis obovatis, antheris flavis, ovariis glaberis, stylis filiformibus, stagmatibus capitatis vel clavatis; stylopodium deficiens; discus praesens; fructus teres vel dorsaliter compressum late oblongus, commissura non constricta, alatis, crassis, margine acuto vel rotundato laevi; carpophorum bipartitum deciduus; superficies commissuralis planus vel navicularis; vittae in intervallis 1 in commissura 2.

Plants acaulescent, tufted, weakly or not aromatic; taproot 0.3–2.2 cm in diameter near summit (deep seated). **Stems:** caudex simple or branched, clothed with persistent leaf bases or remnants of vascular strands, pseudoscape absent, rhizomes absent. **Leaves** herbaceous, stiffly so, somewhat fleshy, glabrous or minutely scabrous on margins (20×), not viscid, green; petioles 1–10 cm long; blades broadly lanceolate to ovate or broadly ovoid in outline, 2–6 cm wide (if pressed flat), 4–18 cm long, 1-pinnate or 2-pinnate at least in part, sometimes more highly compound yet in a similar fashion, leaflets often opposite on rachis or opposite on side axes if present, axes and rachis terminating in 2 or 3 leaflets, main axes and ultimately leaflets ascending 5–30 degrees, sometimes arcuately so, from rachis and also directed adaxially at a 20–45 degree angle from one another, thus leaf not planar but 3-dimensional or V-shaped when observed along rachis with adjacent branches; leaflets sessile, 5–70 mm long, often with a solitary midrib, mostly 0.8–1(–2) mm wide, filiform to narrowly linear and entire, not or little overlapping, apices sharply acute to usually spinulous, tan to whitish, cartilaginous. **Peduncles** (4–)7–40 cm long, glabrous except sparsely to moderately puberulent at apex with peg-like hairs (20x) appearing glandular; involucre absent, rays 6–24, 3–8 mm long, lengthening slightly in fruit; **Inflorescences** of 1–5(–11+) flowering stems, each terminated by an umbel, congested, convex to globose, 2–3.5 cm wide; umbellets mostly andromonoecious of 2–8 staminate and 2–5 (or more) perfect flowers; involucel weakly dimidiate, of 5–7 bractlets, linear, entire, 1–3 mm long, distinct, green, margins narrowly scarious; pedicels 1–1.5 mm long, to 3 mm long in fruit. **Flowers** yellow (fading to pale yellow or white); sepals 0.2–0.4 mm long, deltoid to oblong, papery, or obscure especially in fruit; petals 1–1.2 mm long, obovate in lower two-thirds with a narrow, inflexed, plicate apex; anthers yellow, 0.5 mm long; filaments 1 mm long; styles filiform, terete, 0.6 mm long and slightly spreading or 0.8 mm long and arcuate in fruit; stigma capitate to clavate; stylopodium none; disc present. **Fruit** terete to somewhat compressed dorsally, broadly ovoid to oblong, not constricted at commissure, 4.8–5.2 mm long, 2.7–2.8 mm wide on commissure, tan; dorsal wings 0.6–0.8 mm tall, the lateral ones often the tallest, 0.5 mm wide at base, straight, prominently corky, edges acute to rounded, wedge-shaped to truncate-ovate in cross section, smooth throughout; mericarps with commissure planar to curved adaxially from the two ends, often with central groove or even cupulate due to enlargement of wings; oil tubes 1 per interval, 2 on commissure, forming ribbons, ca 0.3 mm wide; carpophores present, split to base (Fig. 2). **Seeds** 1 × 1.1–1.3 mm in cross section, ovoid but broadly so, shallowly sulcate adaxially.

Paratypes: **U.S.A. NEW MEXICO: Rio Arriba Co.:** NE end of Black Mesa, 1 air mi N of Embudo, T23N R9E sec. 14, 6,900 ft, rocky outcrop and slopes, 20 Jun 1980, fruit, *Hartman 11742* (RM), 31 May 1978, flower, *R. Spellenberg 4981* (NMC) [*Aletes sessiliflorus*, determination by L. Constance, UC]; NW of Embudo on N slope of Black Mesa, T23N R9E sec. 14, 15, 6900 ft, rocky slopes with piñon pine and juniper, 1 May 1982, flower, *Hartman 13954 & G. Fonken* (RM); 6 air mi SE of Dixon, T22N R10E sec. 1, 6,380 ft, sandy draw and stream bottom, 22 May 2006, fruit, *Hartman 82106* (RM); NE end of Black Mesa, 1.5 air mi, NNE of Embudo, T23N R9E sec. 14 SW¼, sec. 15 SE¼, 11 May 2006, flower, fruit, *B.E. Nelson 67772* (RM). **Taos Co.:** Hondo Canyon along Forest Road 606, SE of NM hwy. 68, up Hondo Canyon Creek 0.6 air mi, T24N R12E sec. 30, NE¼, 7600–8450 ft, SW exposure, rocky slope with ponderosa pine and Douglas fir, 17 May 2005, flower, fruit, *Hartman 80487 & Larson* (RM); Cebolla Mesa Campground and overlook at end of Forest Road 9 and 0.6 air mi N, T28N R12E sec. 20 W½, 7,380–7,420 ft, piñon/juniper woodland, 18 May 2005, flower, *Hartman 80566 & Larson* (RM), 9 Aug 2009, fruit [100+ mericarps collected from duff below plants], *Hartman 89268* (RM); 0.2 air mi W of Cerro to top of Guadalupe Mountain, T29N R12E sec. 11, 14, 7,560–8,763 ft, piñon/juniper to top with Douglas fir/ponderosa pine, 25 Jul 2005, vegetative, *Hartman 81342* (RM); Brushy Mountain, S half, T29N R11E sec. 34 NE¼, 7,600–7,916 ft, piñon/juniper above, lower slopes with sagebrush and rabbitbrush, 28 Jul 2005, vegetative, *Hartman 81528* (RM); NE slope and summit of Cerro Montoso, T28N R11E sec. 3, W½ sec. 10, E edge of sec. 9, 7,600–8,655 ft, piñon/juniper with some ponderosa pine, 28 Jul 2005, vegetative, *Hartman 81547* (RM); NM hwy. 68 SW of Taos at Arroyo Hondo, T24N R11E sec. 14, 6,598–6,976 ft, half way up canyon towards Rio Grande, 16 May 2006, fruit, *Hartman 81750* (RM); Agua Caliente Canyon from dirt road immediately S to BLM land and bottom of canyon, T23N R11E sec. 3, 4, 6200–6,700

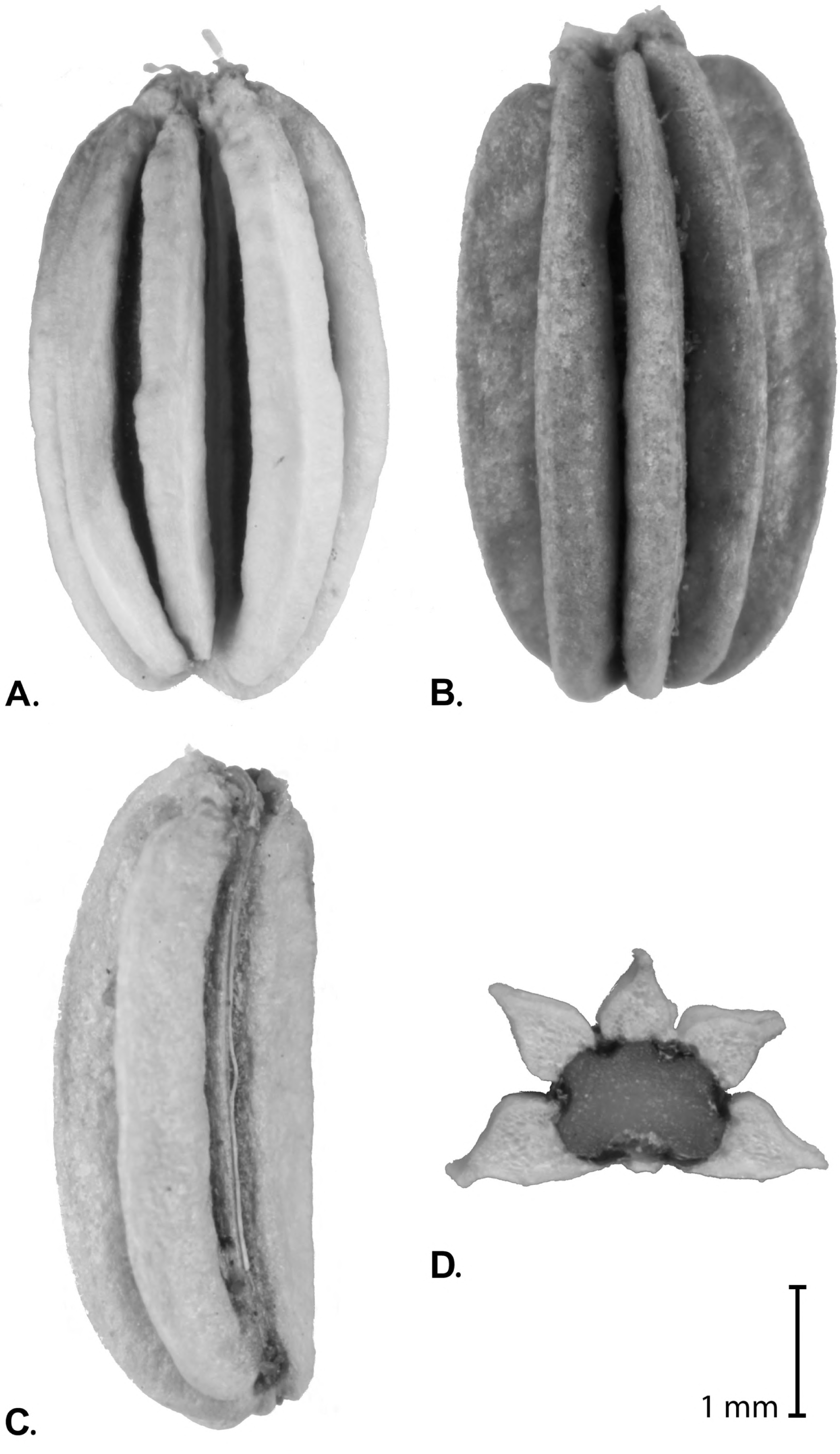

Fig. 2. Detailed morphological features of *Cymopterus spellenbergii.* A. Fruit in side view with the commissure faintly visible down the center (*Sivinski 7613*, RM). The remaining images are based on *Hartman 11742* (RM). B. Dorsal view of mericarp. C. Mericarp in partial side view; upper part of the deciduous carpophore branch attached at apex. D. Cross section of mericarp, oil tubes evident.

ft, piñon/juniper above and on slopes, some cottonwoods in canyon bottom, 19 May 2006, vegetative, *Hartman 81846* (RM); Harding Mine [pegmatite mining], 4.7 air mi WSW of Picuris Pueblo, T23N R11E sec. 29 S½ (36.1945°N, 105.7947°W), 7,300 ft, north-facing slopes of rocky sandy loam soil from metamorphic rock in piñon-juniper woodland, 16 Jun 2010, fruit, *R.C. Sivinski 7613* (RM, UNM).

Etymology.—This species is named for Richard Spellenberg of New Mexico State University who discovered it and for his studies on legumes and nyctages and of the flora the Sierra Madre Occidental, Mexico.

Distribution and ecology.—*Cymopterus spellenbergii* has been documented from the vicinity of the Rio Grande in two general areas (Fig. 3). One is in north central Taos County where it is known from four sites west of Questa. The other is in the southwest portion of that county at four locations and two just to the southwest in Rio Arriba County, all northeast of Española. Of the last two sites, the one indicated by the large star marks the type locality. It has been collected several times here and in a radius of one to two mile. Much of the public lands between these two centers of distribution and immediately adjacent to the Rio Grande have been searched for additional populations. Additional searches especially on private lands are warranted.

Cymopterus spellenbergii typically is found growing on basalt of the Servilleta Formation (5.6 to 4.5 mya) or their degradation products. These volcanic flows cover much of the Taos Plateau or form caprock along canyons rims. The novelty may also occur in sandy draws below the caprock. In one case it has been documented growing on metamorphic (*R.C. Sivinski 7613*).

Typically this species is found in plant communities dominated by piñon pine and juniper or by ponderosa pine and Douglas fir.

Phenology.—*Cymopterus spellenbergii* generally flowers from the end of April to late May; fruits from mid May to early July. As noted above, mature mericarps can be found below plants in mid August if there is adequate plant material covering the ground to hold them in place.

Conservation.—*Cymopterus spellenbergii* fits criteria for a species of conservation concern and may be so recognized by the New Mexico Rare Plant Technical Committee and Natural Heritage New Mexico.

Notes.—The closest known sites for *Cymopterus sessiliflorus* (*C. breviradiatus* included) is about 35 air miles due west of the type locality of *C. spellenbergii*. It was collected at three locations in the vicinity of Ghost Ranch near Canjilon Creek, 3 to 4 miles north of Abiquiu Reservoir (*Larson 5023, 5024, 10348*; RM). These locations are about 30 air miles northeast of the type locality of *C. sessiliflorus*. The habitat was dry, sandy bottom and rocky sides of wash or riparian areas in shales and sandstones of Chinle and San Rafael groups. Sandstone and shales and their erosional products are the most common substrate for this species, especially in dissected landscapes.

A reason for the delay in describing this novelty, and others in the past, is the senior author's insistence on understanding the geographic distribution and morphological variation in adequate detail. Similarly as with *Cymopterus constancei* R.L. Hartm., a nearly thirty year gestation period occurred. In this latter case the taxon was found to occur in five states and the number of specimens documenting its distribution was more than doubled (Hartman 2000). Between 2001 and 2006 (Reif et al. 2009), more than 35,000 numbered collections were obtained in inventories of the Valles Caldera National Preserve, the Santa Fe National Forest, the Carson National Forest, and the Taos District of the Bureau of Land Management, all in north central New Mexico.

These studies are part of the larger effort through the Rocky Mountain Herbarium (RM) to produce a critical flora of the Rocky Mountains and to map, based on vouchered specimens, the distributions of its taxa in relatively fine detail (Hartman 1992; Hartman & Nelson 2008; Hartman et al. 2009).

This inventory of north central New Mexico allowed for detailed searches for *Cymopterus spellenbergii* in the area where it is now known to occur, but also in a vastly larger region with associated ecological diversity. Furthermore, work in south central Colorado (Elliott 2000) had led to the pursuit of the Colorado endemic *Neoparrya lithophila* Mathias (Apiaceae) in New Mexico. Thus both were sought simultaneously. Subsequently it was discovered in New Mexico, near the Rio Grande about ½ mile south of Colorado (Hartman et al. 2006; O'Kane 1988).

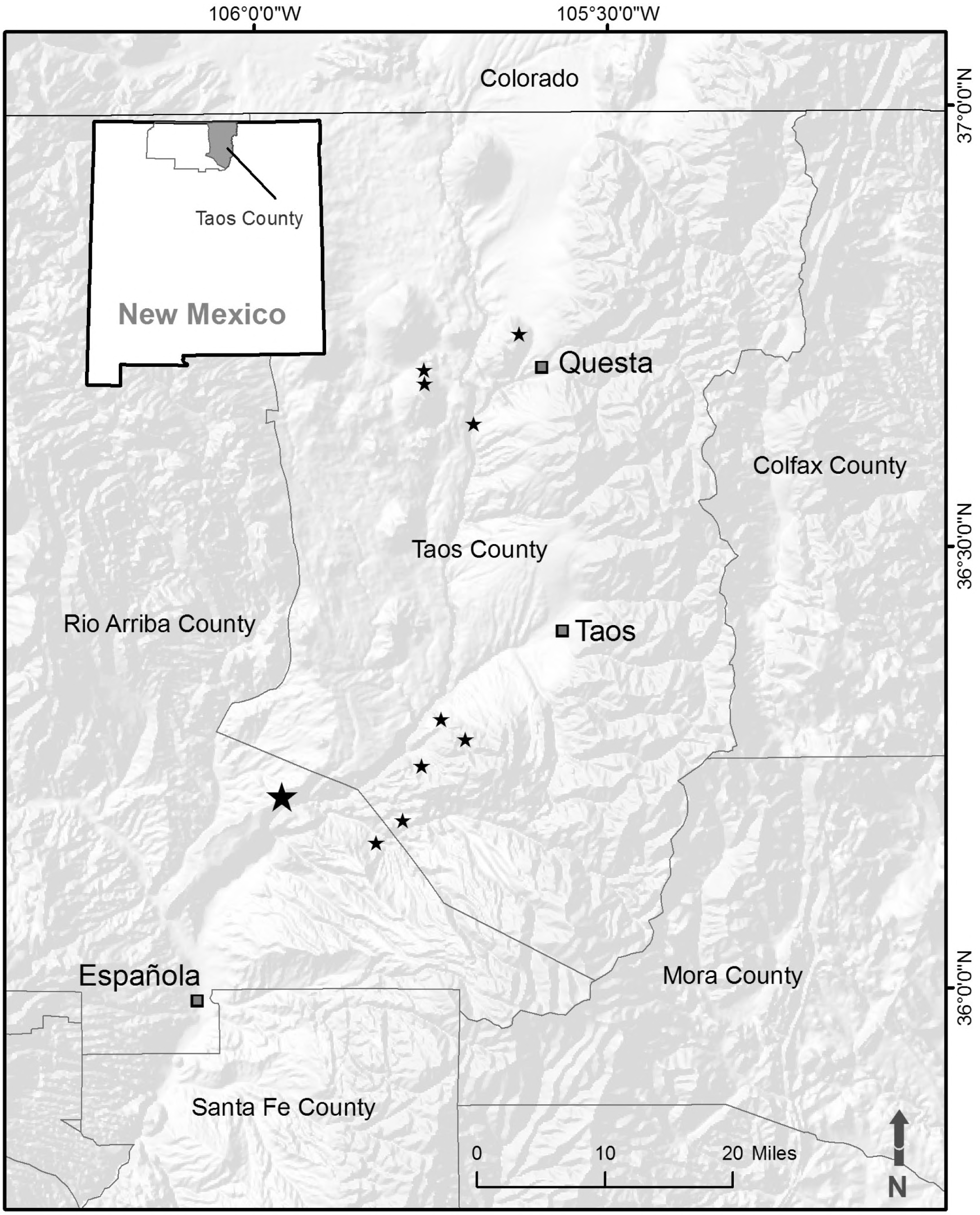

FIG. 3. Geographical distribution of *Cymopterus spellenbergii*. The star represents the type locality.

A series of molecular studies on the perennial taxa of Apiaceae (Apioideae) endemic to western North America have been published by Stephen R. Downie's Lab at the University of Illinois (Downie et al. 2002; Sun 2003; Sun et al. 2004; Sun and Downie 2004, 2010a, 2010b). The accession *Hartman 13954* (RM) was misidentified by Hartman as *Aletes sessiliflorus* (here treated in *Cymopterus*) and was not corrected subse-

quently. In fact, it represents *C. spellenbergii* from the type locality. Furthermore, three accessions labelled *Aletes macdougalii* subsp. *breviradiatus* are here recognized as *C. sessiliflorus*. All three of these collections are from the western part of the geographic range.

Most molecular analyses were based on nuclear ribosomal ITS and chloroplast *rps*16 intron and *trn*F-L-T sequences. Sun and Downie (2010a, Figs. 2, 3) also included morphological characters (proportionally weighted). As stated, "these trees are largely congruent with those trees derived from molecular data alone (Sun 2003; Sun and Downie 2010b). In fact these trees are better resolved and, in general, their branches are more strongly supported than any phylogenetic tree for the group heretofore available. …" In these papers, subclade 3f depicts *C. spellenbergii* and *Harbouria trachypleura* (A. Gray) J.M. Coult. & Rose as strongly supported sister taxa with *C. bakeri* (J.M. Coult. & Rose) M.E. Jones (as *Oreoxis*) being sister to this clade followed by *Cymopterus filifolius* (Mathias, Constance, & W.L. Theob.) B.L. Turner (as *Aletes*) and then *Cymopterus longiradiatus* (Mathias, Constance, & W.L. Theob.) B.L. Turner (as *Pseudocymopterus*) as successively basal branching linages. All five species occur in New Mexico but only *C. spellenbergii*, *C. filifolius*, and *Harbouria trachypleura* have filiform to linear leaflets. Subclade 3c has one taxon that consistently has linear leaflets (*Cymopterus davidsonii* (J.M. Coult. & Rose) R.L. Hart.) and another that occasionally does (*Cymopterus lemmonii* (J.M. Coult. & Rose) Dorn). Thus only five taxa from New Mexico in Clade 3 (41 accessions) has or may have this feature. *Cymopterus sessiliflorus* (as *Aletes macdougalii* subsp. *breviradiatus*) is in subclade 1g (Clade 1 consists of 60 accessions) and is quite distant phylogenetically from subclades 3f and 3c. The conclusion is that *C. spellenbergii* is always associated with the taxa in subclade 3f and does not represent *C. sessiliflorus* (subclade 1c).

The concluding paragraph of Sun and Downie (2010a) discusses the recent trend of including related genera in *Cymopterus* stating that "given this trend and overlapping [morphological] character variation among genera, it may very well be possible that future studies will indicate that all or most members of the group [perennial endemic North American apioids] should be combined into one large, polymorphic genus, an extreme but possibly inevitable action."

A key is provided for the species of Clade 3 (Sun and Downie 2010a) that have or may have filiform to linear leaflets and occur at low to mid elevations in New Mexico. Where a combination is available under the genus *Cymopterus*, that name is used. Many of these combinations were made by Turner (1998). *Cymopterus sessiliflorus* (*Aletes macdougalii* subsp. *breviradiatus*) in Clade 1 is included for comparison. *Cymopterus davidsonii* has been collected sparsely, especially in fruit. Thus its differentiation from *C. lemmonii* needs clarification.

1. Plant acaulescent.
    2. Peduncles glabrous throughout or slightly scabrous above; fruit with membranous wings (*Aletes macdougalii* subsp. *breviradiatus*) ____ **C. sessiliflorus**
    2. Peduncles minutely puberulent (20x) with peg-like hairs at apex; fruit with thick, corky wings or ribs ____ **C. spellenbergii**
1. Plants caulescent with 1 or 2 reduced leaves subtending branch(s).
    3. Fruit minutely papillate at least between the wings.
        4. Fruit subterete (*Pteryxia davidsonii*) ____ **C. davidsonii**
        4. Fruit dorsally flattened (*Pseudocymopterus montanus*) ____ **C. lemmonii**
    3. Fruit glabrous or densely warty throughout.
        5. Fruit smooth (*Aletes filifolius*) ____ **C. filifolius**
        5. Fruit prominently and densely warty ____ **Harbouria trachypleura**

Cymopterus spellenbergii and *C. filifolius* are very similar in appearance but may be differentiated by the characters in the key. Furthermore, the latter has more highly dissected leaves and the sepals in fruit elongate and become indurate, often with one or more hooked inward (versus deltoid to obsolete, papery, not enlarging in fruit). A generality can be made regarding the substrate on which these three species occur: *C. spellenbergii* grows primarily on or adjacent to basalts, *C. filifolius* grows primarily on limestone but sometimes on rhyolite or other volcanics, and *C. sessiliflorus* is found on sandstones and shales. The distribution of *C. filifolius* is to the south of *C. spellenbergii* by at least 100 miles in eastern Torrance County on the east slope of Manzano Mountains and in northeastern Socorro County in the Los Pinos Mountains. It has been collected in both

counties on Chupadera Mesa. To the south and southeast it has been documented also in Dona Ana, Eddy, Lincoln, and Luna counties, New Mexico, and in Brewster, Culberson, Davis, and Hudspeth counties, Texas.

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A NEW HYBRID OF *HIBISCUS* (MALVACEAE) FROM TEXAS

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ABSTRACT

A new naturally occurring hybrid between *Hibiscus coulteri* and *H. denudatus* is described and named **H. ×sabei** Weckesser. Morphological and pollen stainability evidence is presented.

RESUMEN

Se describe un nuevo híbrido natural entre *Hibiscus coulteri* y *H. denudatus* que se nombra **H. ×sabei** Weckesser. Se presentan pruebas morfológicas y tinción del polen.

Apparent hybrids between *Hibiscus coulteri* Harv. ex A. Gray and *Hibiscus denudatus* Benth. have been found in the Big Bend region of Brewster County, Texas, with five locations supporting a total of seven plants. Each location also hosts populations of *H. coulteri* and *H. denudatus*. Natural hybridization between other species of *Hibiscus* has been reported previously (e.g., Martin 1971; Chang 1991; Klips 1999).

Hibiscus ×sabei Weckesser (*H. coulteri* × *H. denudatus*), hyb. nov. (**Figs. 1, 2**). Type: U.S.A. Texas: Brewster Co.: Terlingua, 2 mi W of Terlingua Ghost town on FM 170 at Long Draw, disturbed gravelly limestone soil, roadside, in association with *H. coulteri*, *H. denudatus*, elev. 3005 ft, N29.19.124 W103.38.884, widely branching stems from woody base, leaves 3-lobed, flower purple to white with purple edges and streaking, possible cross between *H. coulteri* and *H. denudatus*, 28 Oct 2005, *Weckesser 645* (holotype: SRSC; isotype: SRSC).

Differt a *Hibiscus coulteri* et *H. denudato* floribus albis, trichomatibus stellatis radiis 3–6 ad 1 mm in longitudine, bracteis quam sepalibus dimidio brevioribus, et trichomatibus stigmatum usque ad 1 mm in longitudine. Differt a *H. denudato* foliis tripartitis profunde dissectis.

Plants suffruticose; stems erect to ascending, older stems brown with longitudinal grooves; lower leaves 15 mm long, 12 mm wide, occasionally entire, ovate to cordate with dentate margins, upper leaf blades (13–)15–20(–22) mm long, tripartite with dentate margins, both with moderately spaced stellate hairs with 3–6 radially arranged rays, each ray to 1 mm long; petioles similarly stellate; axillary flowers few to many; bracts 9–10, linear, 7–9 mm long, approximately half as long as calyx lobes, abaxial surface with stellate hairs as described, adaxial surface glabrous to sparsely hispid, margins antrorsely hispid; pedicels (10–)25–45(–65) mm long; calyx lobes 5–6, acute, lanceolate, 15–17 mm long, abaxial surface with dense stellate hairs as described, adaxial surface and margins antrorsely hispid; petals 5, obovate, 30 mm long, creamy white with purple-tinged margins, petal base yellow with or without maroon spot, drying when pressed to mottled purple and white or yellow; staminal column 5.5–7 mm long, anthers pale yellow to white; stigmas maroon, with hairs to 1 mm long, on style branches 2.5–3 mm long; capsule nearly glabrous, apically hispid with few hairs along loculicidal sutures; seeds 3 mm long, sericeous, hairs 3–5 mm long, completely obscuring seed surface.

Additional specimens examined: **U.S.A. TEXAS. Brewster Co.:** Terlingua, Hwy 170, 6 mi W of Hwy 118, gravelly limestone on limestone outcrop, old road cut, 27 Apr 2007, *Weckesser 1019* (SRSC); Terlingua, Hwy 170, 6 mi W of Hwy 118, gravelly limestone on limestone outcrop, old road cut, 18 May 2007, *Weckesser 1020* (SRSC); Terlingua, Hwy 170, 6 mi W of Hwy 118, gravelly limestone on limestone outcrop, old road cut, 18 May 2007, *Weckesser 1021* (SRSC); Terlingua, Hwy 170 at Long Draw, on highway shoulder, limestone gravel, 25 May 2007, *Weckesser 1023* (SRSC); Terlingua, Hwy 170 at E Terlingua Ghosttown turnoff, roadside on clay soils with limestone rubble on surface, 23 Jun 2007, *Weckesser 1039* (SRSC); Big Bend National Park, River Road East, 0.15 mi S of Tornillo Creek, 0.36 mi N of Gravel Pit turnoff, 100 ft from road, 29 May 2007, *Alex 108*, BIBE 43087, Accession #BIBE-01493 (SRSC).

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Fig. 1. (above) Flower of *Hibiscus* ×*sabei*, Hwy 170 at Long Draw, 2 Oct 2007. Photograph by author.
Fig. 2. Flower buds of *Hibiscus* ×*sabei*, Hwy 170 at Long Draw, 6 April 2007. Note relative sizes of sepals and bracts. Photograph by B. Alex.

KEY TO *HIBISCUS* IN WEST TEXAS

1. All leaves entire; hairs with more than 6 radially arranged rays; flowers pale purple _____**Hibiscus denudatus**
1. Lower leaves entire, upper leaves tripartite, deeply dissected; hairs with 6 or fewer rays, variously arranged; flowers yellow or white.
    2. Hairs with 4 rays arranged in pairs longitudinally along stem; flowers yellow_______ **Hibiscus coulteri**
    2. Hairs with 3–6 radially arranged rays; flowers white tinged with purple _____________ **Hibiscus ×sabei**

Distribution.—Five apparent hybrids in three sites were documented in the vicinity of Terlingua, and Big Bend National Park (BBNP) hosts apparent hybrids in two locations, one plant along the East River Road and one plant, known only from photographic record, along the Cattail Falls trail. Each site has been disturbed by either natural erosion patterns or man-made highway construction. The

parent species are sympatric across most of their ranges (Correll & Johnston 1979; Fryxell 1988; Turner et al. 2003). *Hibiscus coulteri* is found from California to West Texas and in adjacent Mexico. *Hibiscus denudatus* is found from Arizona to West Texas and in adjacent Mexico.

Previously, a suspected hybrid was collected in the vicinity of the Eagle Mountains in Culberson County, Texas (*Warnock, Johnston & Powell 17991* SRSC). Close examination of that specimen revealed characters that match those of *Hibiscus coulteri* and not those of the hybrid described here. No other *Hibiscus* collections in SRSC share the characteristics of the hybrid. No hybrid specimens were uncovered as a result of a search of the *Hibiscus* collections at TEX. Possible occurrences of hybrids in other areas where populations of both species exist warrant further attention. Further herbaria searches may yield as-yet unrecognized collections of the hybrid.

Morphology.—The suspected hybrid was first noticed by the color of its flower, creamy white with purple streaking along the margins of the petals (Fig.1). In the Big Bend area, the observed color for *H. coulteri* is a pale to bright yellow, and for *H. denudatus* lavender to pale purple-pink. When dried, the flowers of the hybrids tend to turn purple with some white mottling. An exception to this is seen in the collection from BBNP (*Alex 108* SRSC). The flower dried predominantly yellow with purple mottling. It can be seen in herbarium specimens (SRSC) that the flowers in each of the parent species tend to retain, with some fading, their original color when pressed. Purple streaking occurs in some herbarium specimens of *H. coulteri* (SRSC). In published descriptions of the parent species, the petals of *H. coulteri* are variously described as "whitish to lemon- or sulfur-yellow and commonly reddish- or purple-tinged" (Correll & Johnston 1979), "usually yellow, perhaps whitish or purple-tinged" (Powell 1998), and "yellow with a small (often striate) maroon spot at base or spot absent" (Fryxell 1988). In *H. denudatus*, the petals are "lavender-purple" (Correll & Johnston 1979), "lavender to purplish" (Powell 1998), or "lavender or white" (Fryxell 1988). Normal petal color variation in the parent species may explain the petal color in the hybrid and the variation seen in the pressed hybrid flowers.

In the absence of flowers, the hybrid plants exhibit gross characteristics of *H. coulteri*: few to several stems arising from a woody root, some lower leaves entire, ovate to cordate with dentate margins, and upper leaves deeply three-lobed. Given these similar characters, the white flowers might be seen as pigment variability within the species. Upon closer examination, however, the hybrids consistently exhibit intermediate forms for hair, sepal, and bract characters. Because there is a marked difference in the characters of the parent species, it is possible to identify the intermediate forms of these characters in the hybrid.

The hairs of the parent species are distinct. In *H. coulteri* the stellate hairs have 4 long rays, up to 1 mm, sometimes obvious without magnification, "aligned 2-by-2 longitudinally with the stem axis" (Fryxell 1988), with sufficient overlap on stems and petioles to produce a hirsute appearance. *Hibiscus denudatus* also has stellate hairs, but the rays are numerous, arranged radially, and much shorter than those of *H. coulteri*. The stellate hairs are so densely distributed that leaves, petioles, and stems appear tomentose. In contrast to the parent species, the hairs of the hybrid resemble those of *H. coulteri* in length of the rays, but with 3–6 rays arranged radially as in *H. denudatus*.

In *H. coulteri*, the bracts are nearly as long as the sepals (up to 20 mm). In *H. denudatus*, the bracts (no longer than 4 mm) are markedly shorter than the sepals (11–15 mm), less than half their length (Fryxell 1988). In the hybrid (Fig. 2), the bracts (7–10 mm) are intermediate between the parent species and are usually just over half the length of the sepals (15–17 mm).

The differences in fruit and seed characters between the parent species are narrowly defined. There is a degree of overlap that precludes using these characters in distinguishing the hybrid plants from the parent species. The fruits of *H. denudatus* are globose and glabrous or pubescent at apex. The fruits of *H. coulteri* are ovoid and antrorsely hispid apically (Correll & Johnston 1979; Fryxell 1988). The fruits of the hybrids do show some pubescence apically. The only marked difference seen in the few hybrid fruits available for observation is that they seem to be laterally compressed, which may indicate incomplete development of carpels or incomplete seed development. The seeds of both parent species are sericeous, completely covered

in fine silky hairs, with seed length 0.5 mm longer and hair length 1 mm longer in *H. coulteri* than *H. denudatus* (Fryxell 1988). The seeds of the three entities are barely distinguishable in general appearance and length of hairs, the dimensions of the hybrid seeds falling within the ranges of the two parent species for both seed and hair length.

Pollen stainability.—Pollen stainability tests, using aceto-carmine solution (M. Powell pers. comm.; Snow 1963), showed that the pollen from the hybrid had 40–50% stainability, indicating low viability. This is as expected in F_1 hybrids (M. Powell pers. comm.).

Etymology.—*Hibiscus ×sabei* is named for Ken "Sabe" Smith, a keen observer of the wildflowers of Big Bend, who brought this unusual desert mallow to the author's attention.

Comments.—Given the polyphyletic nature of Malvaceae, it is worth mentioning that *Hibiscus coulteri* and *H. denudatus* are both in section *Bombicella* of the genus (Fryxell 1980). A chromosome number for *H. denudatus* (2*n*=22) has been published (Fryxell 1988), but there is no published number for *H. coulteri*. Attempts to determine the chromosome number for *H. ×sabei* were unsuccessful.

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CAREX AUSTRODEFLEXA (CYPERACEAE), A NEW SPECIES OF *CAREX* SECT. *ACROCYSTIS* FROM THE ATLANTIC COASTAL PLAIN OF THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Carex austrodeflexa (sect. *Acrocystis*) is described from the coastal plain of the southeastern United States. This species inhabits distinctive wetland communities in streamheads and small-stream swamps, usually under seepage influence. It is the only wetland member of section *Acrocystis* found in the southern Atlantic and Gulf Coastal Plain. It may be told from the morphologically similar *Carex deflexa* on the basis of its loosely cespitose habit with long, slender, reddish rhizomes, papillose, glabrate, elliptic perigynium, longer perigynium beak, and longer staminate scales and spikes.

RESUMEN

Se describe **Carex austrodeflexa** (sect. *Acrocystis*) de la llanura costera del sureste de los Estados Unidos. Esta especie vive en comunidades de humedales en cabeceras de arroyos y pantanos de pequeños arroyos, usualmente bajo influencia de filtraciones. Es el único miembro de humedales de la sección *Acrocystis* que se encuentra en el Atlántico sur y la llanura costera del golfo. Puede diferenciarse del morfológicamente similar *Carex deflexa* por su hábito cespitoso con rizomas largos, delgados y rojizos, periginio papiloso, glabro, elíptico, pico del periginio más largos, y escamas estaminales y espigas más largas.

Botanical and ecological studies during the 1990s of the fire-maintained vegetation of the Atlantic and Gulf Coastal Plain of the Southeastern United States uncovered a distinctive species of wetland sedge in the genus *Carex*. Remarkably, this entity was independently discovered by the six authors of this paper. This unfamiliar *Carex* was clearly a member of the section *Acrocystis,* due to the combination of pistillate spikes produced on short, subradical peduncles and an elongate lower pistillate bract. In most characters it keyed to *Carex deflexa* Hornem. Closer examination of the material, combined with additional field and herbarium searches, revealed a number of distinctive features. It became apparent that this entity did not match any of the species descriptions in the most recent complete treatment of section *Acrocystis* (Crins & Rettig 2002). The new species is described as follows:

Carex austrodeflexa P.D. McMillan, Sorrie, & van Eerden, sp. nov. (sect. *Acrocystis*). (**Figs. 1, 2**). Type: U.S.A. NORTH CAROLINA. Pender Co.: common to locally abundant in seepage influenced areas in ecotone of calcium-influenced *Pinus palustris*-mixed graminoid wet savanna and non-alluvial swamp forest, SE of Maple Hill and just S of Lee Road, 12 Apr 1998, *P.D. McMillan 2788* (holotype: NCU; isotypes: MICH, US, USCH).

Carici deflexae Hornem. similis sed differt perigynii rostro longiore ac parietibus valde papillosis praeter rostrum aliter glabris et spica staminata longiore latiore.

Plants perennial, moderately to loosely cespitose by means of slender rhizomes (2.5–)6–9(–12) cm long, 0.7–1.1 mm thick, covered with red or maroon-red sheaths at time of flowering. Leaves predominantly basal, much exceeding culms, principal leaves 11–42 cm long, 1.1–2.4 mm wide, linear, acuminate, sca-

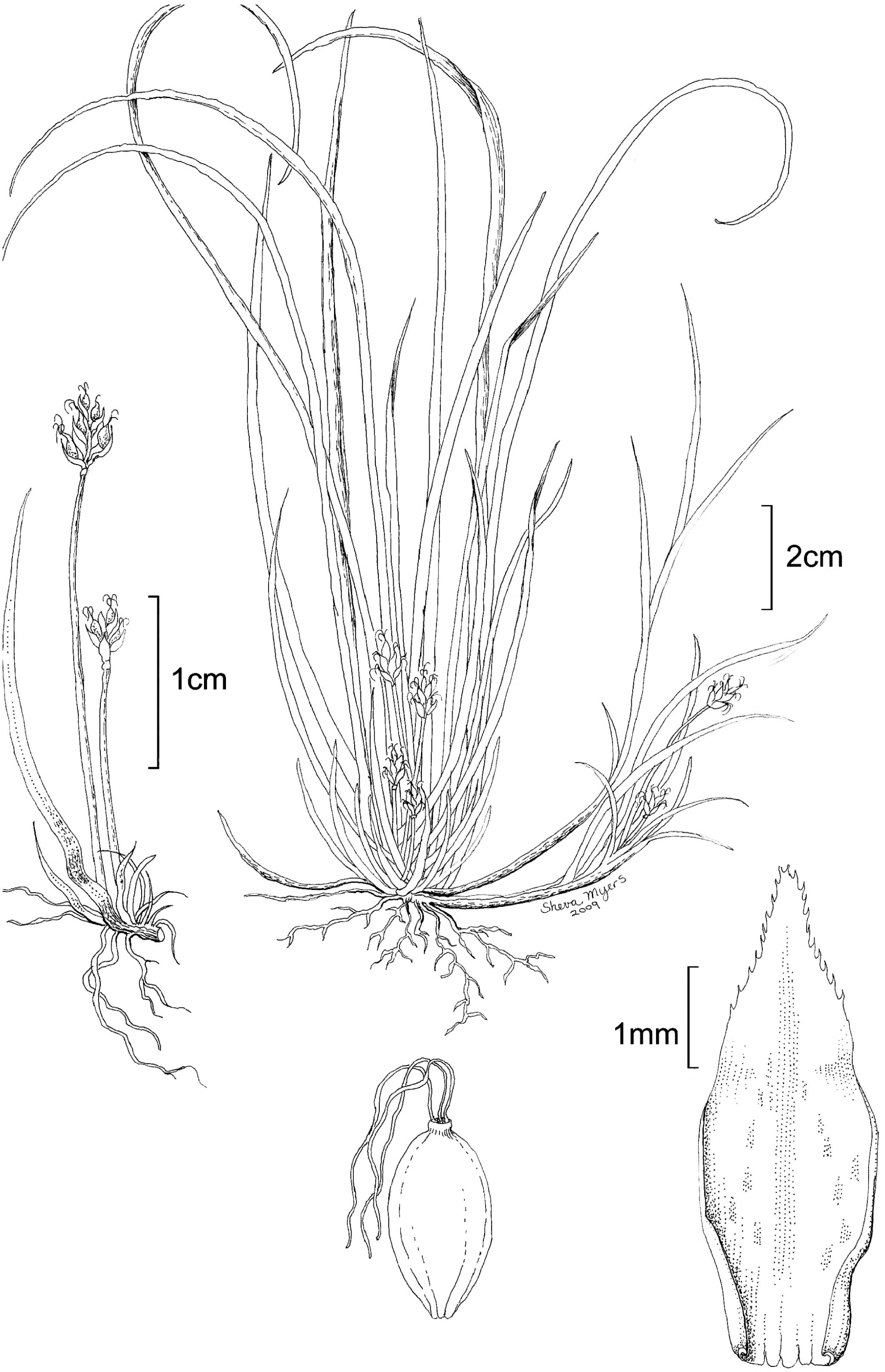

Fig. 1. ***Carex austrodeflexa*** **plant; detail of culms with spikes; pistillate scale; achene. Drawing by Sheva Myers.**

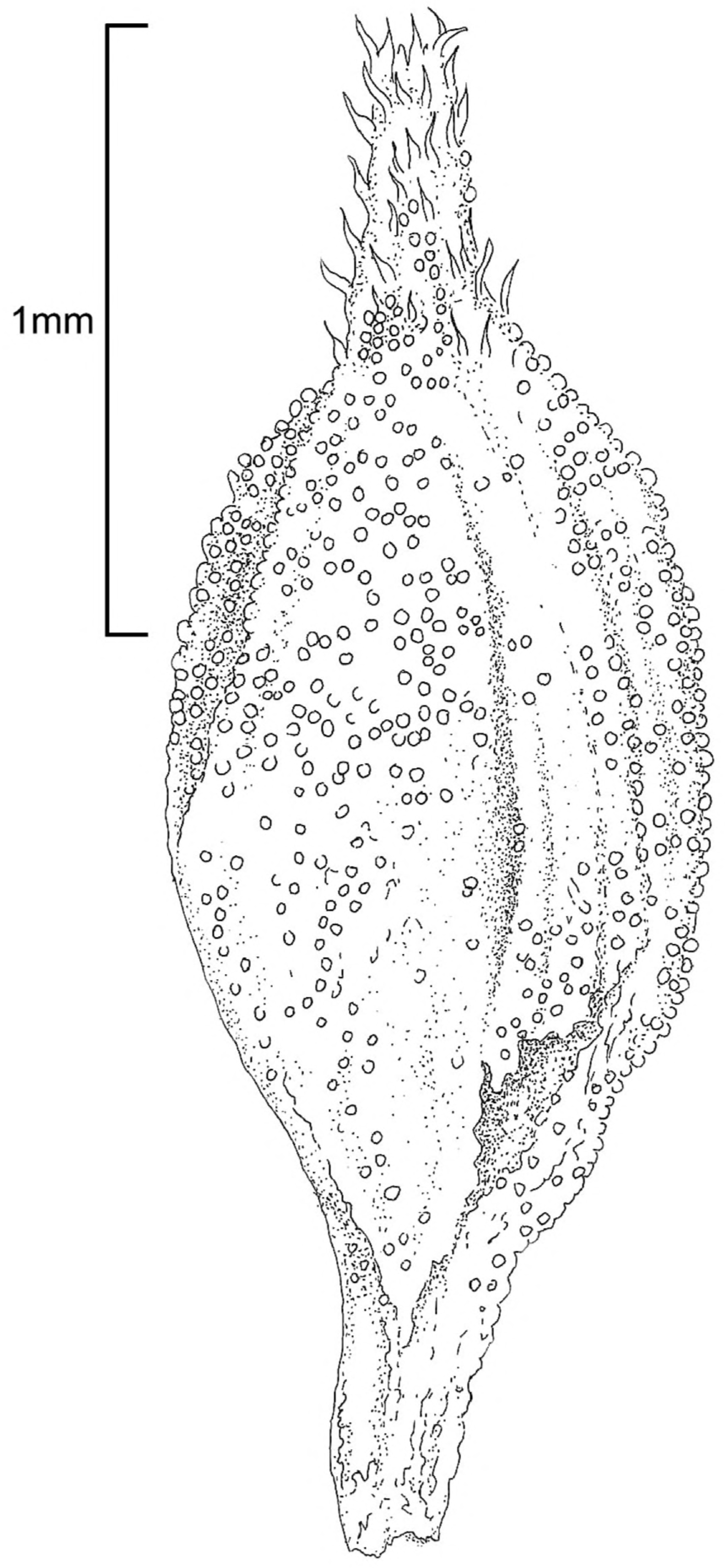

Fig. 2. ***Carex austrodeflexa*** **perigynium. Drawing by Dot Wilbur.**

bridulous on margins and weakly so on abaxial surface. Leaf sheaths loose, white-hyaline with red stripes, ligule 0.3–0.5 mm long, membranaceous, translucent. Fertile culms often surrounded by fibrous remains of previous years' leaves, but not densely so, erect to ascending, 3.4–11 cm tall, 0.3–0.9 mm wide, trigonous, somewhat compressed (especially proximally), margins scabridulous. Inflorescence with 1 terminal linear staminate spike, closely aggregated with (1–)2(–3) pistillate spikes; 1–2 additional pistillate spikes produced on slender basal peduncle(s) 3–11 mm long, these spikes exsert 0–4 mm from leaf sheaths. Cauline pistillate bract shorter than, subequal to or exceeding staminate spike, 3.0–29 mm long, the margins antrorsely scabridulous. Pistillate spikes subsessile, broadly oblong to orbicular in outline, 4–8(–10)-flowered. Pistillate scales narrowly ovate, 2.1–4.2 mm long, 0.9–1.3 mm wide, short-acuminate to short-awned, awn antrorsely scabridulous, scale body stramineous or hyaline, sides often lightly reddish tinged, with prominent green midrib, midrib becoming somewhat keeled distally. Staminate spikes 3–9 mm long, 1–2 mm thick. Staminate scales lanceolate, 2.6–4 mm long, 0.9–1.4 mm wide, acute to short-acuminate, ranging in color from deep red to stramineous, nearly always red at anthesis, with prominent green midrib. Perigynia composed of a body, beak, and stipe-like base; body filled by achene, translucent, surface densely papillose, glabrate to glabrous, hairs minute and restricted to beak and distal end of perigynium. Perigynia 2.4–3 mm long, 0.7–1.1 mm wide, body elliptic to narrowly obovate, 1.3–1.5 mm long, tapering at both ends to a bidentate antrorsely

toothed beak 0.6–1 mm long and a stipe-like base 0.6–1 mm long. Achenes 1.2–1.4 mm long, 0.6–0.8 mm. wide, ovoid, trigonous with convex sides, castaneous to caramel brown, surface faintly cancellate. Style exserted from perigynium beak up to 2 mm, stigmas 3, to 1.3 mm long, straight to curved but not coiled.

Additional specimens examined. BAS refers to personal herbarium of B.A. Sorrie, RJL refers to personal herbarium of R.J. LeBlond. **ALABAMA. Baldwin Co.:** under powerline N of US 90, 2 mi W of Seminole, uncommon in wet seepage slope with *Aristida beyrichiana, Andropogon glomeratus, Lophiola americana*, 12 Mar 1996, *BA Sorrie 8708* (AUA, NCU). **FLORIDA. Gadsden Co.:** streamhead of Lodge Creek, W of Lake Talquin, N of route 20, common under *Liriodendron tulipifera, Illicium floridanum, Magnolia virginiana, M. grandiflora, Ilex coriacea*, 27 Mar 2002, *BA Sorrie 10845* (CLEMS, FSU, GH, NCU). **Okaloosa Co.:** Eglin Air Force Base, frequent in wet loamy sand in shaded steephead of Bull Creek under *Cliftonia* and *Illicium*, 12 Mar 1994, *LC Anderson 14662* (FSU); Eglin Air Force Base, wet peaty sand in shaded *Cliftonia* thicket in Bull Creek steephead, with *Sarracenia rubra* and *Pinguicula primuliflora,* 12 Mar 1994, *LC Anderson 14666* (FSU). **GEORGIA. Richmond Co.:** Fort Gordon, wet streamhead, 23 Apr 1995, *B van Eerden 1289* (DUKE, GA, GH, NCU). **LOUISIANA. Lincoln Co.:** woods near US 80, 8 mi W of Calhoun, 16 Mar 1967, *RD Thomas 1788* (NCU). **NORTH CAROLINA. Brunswick Co.:** Camp Branch Savanna, off of Myrtle Head Road (SR 1335), 1 May 2002, *RJ LeBlond 5582* (NCU). **Cumberland Co.:** common in sphagnum of forested streamhead, Carver's Creek N of McCloskey Road, 26 May 2010, *BA Sorrie 12589* (NCU). **Gates Co.:** pocosin, 3.7 mi NW of Eure on dirt road paralleling Chowan River, 9 May 1958, *HE Ahles 40380* (NCU). **Harnett Co.:** Fort Bragg Military Reservation, wooded streamhead near powerline E of NC route 87, 18 May 2007, *BA Sorrie 11954* (NCSC, NCU); SW of Reedy's Creek Swamp, streamhead pocosin, frequent over a distance of 150 m under *Nyssa biflora, Liquidambar styraciflua, Liriodendron tulipifera, Pinus serotina*, with leaf litter and sphagnum moss, 18 Jun 2005, *BA Sorrie 11627* (NY, NCU); same place, 29 Mar 2006, *BA Sorrie 11762* (DUKE, MICH, US). **Hoke Co.:** Fort Bragg Military Reservation, Rockfish Creek floodplain, 23 Apr 1994, *B van Eerden 876* (FLAS, GH, NCU, NY, US); Rockfish Creek S of US route 401, E of Raeford, moist floodplain of blackwater stream under *Acer rubrum, Taxodium ascendens, Nyssa biflora, Pinus taeda*, 26 Apr 2004, *BA Sorrie 11214A* (FSU, NCSC, US); Fort Bragg Military Reservation, S side of James Creek, hardwood-loblolly pine swamp along blackwater creek, local on mossy root knolls with *Carex lonchocarpa*, 4 May 1997, *BA Sorrie 9177* (BAS, SWSL); Fort Bragg Military Reservation, Rays Mill Creek, boggy floor of streamhead pocosin with *Arundinaria tecta*, 2 Jun 1994, *BA Sorrie 8005* (BAS, GH, MICH, NCU). **Johnston Co.:** Little Divine Road, seepage savanna in powerline, 23 May 1999, *PD McMillan 3333* (NCU); same place, 25 Mar 2000, *PD McMillan 4398* (CITA, CLEMS, MICH, NCU, USCH). **Lee Co.:** Lemon Springs, seepage areas along railroad, 28 Mar 2000, *PD McMillan 4400* (NCU). **Moore Co.:** headwaters of Nicks Creek, streamhead pocosin community, 26 May 2007, *BA Sorrie 11958* (NCU); Weymouth Woods Sandhills Nature Preserve, tributary of James Creek, streamhead community dominated by *Nyssa biflora, Acer rubrum, Liquidambar styraciflua, Liriodendron tulipifera, Pinus serotina*, 5 Apr 1997, *BA Sorrie 9144* (BAS, GA, Weymouth Woods herbarium); east-W tributary of the outlet creek from Pinebluff Lake, streamhead pocosin with numerous wet depressions, 29 Mar 1997, *BA Sorrie 9142* (NY); W of Eastwood at NC 73 powerline, streamhead seepages, Apr 2000, *PD McMillan 4399* (NCU). **Onslow Co.:** Flat Swamp, off of NC 50, 14 Apr 1995, *RJ LeBlond 4193* (MICH); same place and date, BA Sorrie 8316.5 (NCSC); same place, 26 Apr 1996, *RJ LeBlond 4458* (DUKE); same place, 7 May 1996, *RJ LeBlond 4465* (NCU); Sandy Run Swamp, Cooleys Meadowrue Powerline Site, 13 Apr 1996, *RJ LeBlond 4453* (BRIT); Sandy Run Swamp, Pine Plantation Survey Site, 29 May 1996, *RJ LeBlond 4553* (NCU). **Pender Co.:** The Neck Savanna, off SR 1532, 11 Apr 1990, *RJ LeBlond 1189* (specimen missing); same place, 27 Mar 1991, *RJ LeBlond 1939* (RJL); same place, 13 Apr 1996, *RJ LeBlond 4452* (VPI); same place, 7 May 1996, *RJ LeBlond 4471* (NCU); SE of Maple Hill, seepage influenced ecotone of swamp forest, 11 Apr 1993, *PD McMillan s.n.* (NCU); Shaken Creek Savanna, hardwood drain along E side of Pactolus "Holy Grail" savanna, 26 Mar 2005, *RJ LeBlond 6088* (NCU); **Richmond Co.:** Sandhills Game Land, Joes Creek at SR 1610 bridge, 26 Apr 1994, *B van Eerden 877* (AUA, BRIT, MISS, NCSC, VPI, SWSL, WILLI); same place, 28 Mar 2000, *PD McMillan 4401* (NCU); Sandhills Game Land, gasline N of Tilley Street extension, streamhead community dominated by *Nyssa biflora, Magnolia virginiana*, and sphagnum moss, 6 July 2005, *BA Sorrie 11639* (BAS); Sandhills Game Land, Clay Branch, boggy streamhead with *Carex collinsii*, 6 Jun 1994, *BA Sorrie 8014* (BAS, NCU). **Scotland Co.:** Sandhills Game Land, Scotland Lane Annual Burn Site, 6 Apr 1994, *B van Eerden 848* (NCSC, US); same place, locally abundant, 31 Mar 1997, *PD McMillan 2130* (CLEMS, NCU, USCH); Sandhills Game Land, just N of Scotland Lane, 1 km SW of SR 1328, forming mats in streamhead pocosin, 18 Apr 2000, *PD McMillan 4438* (BRIT, CLEMS, DUKE, FSU, GA, GH, MICH, MO, NCU, NY, PH, VPI); Sandhills Game Land, Bagget Lake Lane at Bones Creek, streamhead pocosin dominated by *Nyssa biflora, Chamaecyparis thyoides, Liriodendeon tulipifera, Magnolia virginiana*, in sphagnum moss with *Rhynchospora leptocarpa*, 4 Jun 2004, *BA Sorrie 11266* (APSC, NCSC); Sandhills Game Land, Tower Branch S of Scotland Lake, streamhead pocosin, scattered on mossy banks of blackwater creek, 20 Mar 1997, *BA Sorrie 9140* (BAS, DUKE); same place, 28 Mar 2000, *PD McMillan 4402* (NCU); Sandhills Game Land, S of Gardner Farm Lane, uncommon on sphagnum knolls in Piney Pools, 24 Jun 1994, *BA Sorrie 8054* (NCSC, NCU); Sandhills Game Land, branch N of Beaver Dam Creek, streamhead with *Arundinaria tecta, Rhynchospora leptocarpa*, 8 Apr 1994, *BA Sorrie 7832* (BAS, FSU, GH, MICH, US); Sandhills Game Land, headwaters of Beaver Dam Creek, 19 Apr 1994, *B van Eerden 873* (NCU, WILLI); Sandhills Game Land, branch S of Little Muddy Creek, common in sphagnum moss under *Arundinaria tecta*, 16 Mar 1994, *BA Sorrie 7815* (BAS, NCSC). **SOUTH CAROLINA. Aiken Co.:** Savannah River Site, N of Road 8-1, floodplain on mossy hump by water, 30 Mar 1994, *PE Hyatt 5810* (MICH); Tinker Creek at SC route 781, 12 Apr 1995, *B van Eerden 1261* (APSC, CLEMS, DUKE, FLAS, GA, MO, NCU, NY, PH, USCH). **Aiken/Barnwell Cos.:** Tinkers Creek, streamhead bordering seepage forest, 12 Apr 1997, *PD McMillan 2206* (NCU). **Barnwell Co.:** Savannah River Site, tributary to Meyer's Branch, hardwoods, 5 Apr 1994, *PE Hyatt 5823* (MICH). **Chesterfield Co.:** Sandhills National Wildlife Refuge, Ham Creek, 23 Apr 1995, *B van Eerden 1290* (CLEMS, FSU, GH, US, USCH); Sand Hills State Forest, Barefoot Seeps, 23 Apr 1995, *B van Eerden 1271* (LSU, MICH, MISS, NCU, NLU, PH, TENN, USCH, VPI); Sand Hills State Forest, streamhead, 2000, *PD McMillan 4403* (NCU, USCH). **Greenville Co.:** Little Pinnacle Mountain, locally abundant along

borders of cataract bog, associated with *Sarracenia purpurea, Parnassia grandifolia, Oxypolis rigidior, Fothergilla major*, 24 May 2001, *PD McMillan 5146* (CLEMS, NCU). **VIRGINIA. Caroline Co.:** Fort A.P. Hill Military Reservation, sphagnous hummocks of forested seepage swamp, with *Carex seorsa, C. collinsii*, and *C. atlantica* ssp. *atlantica*, 1.1 mi SW of Eubanks Corner along headwaters branch of Mill Creek, 17 May 2006, *GP Fleming 15354 with K Taverna* (VPI); Fort A.P. Hill Military Reservation, sphagnous hummocks of sloping sand-bottomed forested seepage swamp, with *Carex styloflexa, Carex atlantica* ssp. *atlantica,* and *Helonias bullata*, 0.65 mi NE of jct Rtes 2 and 629 along spring branch tributary of Turkey Track Creek, 17 May 2006, *GP Fleming 15355 with K Patterson* (VPI). **Isle of Wight Co.:** Blackwater Ecological Preserve, locally common in upper reaches of tributary of river, almost always rooted in mats of bryophytes growing on bases of tree trunks, on old stumps, and similar hummock-type microhabitats, associated with *Liquidambar styraciflua, Liriodendron tulipifera, Acer rubrum, Clethra alnifolia, Lyonia ligustrina, Symplocos tinctoria, Arundinaria gigantea, Woodwardia areolata*, 19 Jun 2001, *JF Townsend 2562* (WILLI).

DISCUSSION

Among eastern North American species of the section *Acrocystis*, the new species keys readily to *Carex deflexa*. Both species produce terminal staminate spikes closely associated with overlapping, subsessile pistillate spikes on the primary (distal) inflorescence and also produce pistillate spikes on short basal peduncles. Both species have long lower pistillate bracts on the primary inflorescence. *Carex austrodeflexa* may be separated from *C. deflexa* by its longer perigynium beak (0.6–1 mm vs. 0.4–0.8 mm) and papillose perigynia, which are normally glabrous or glabrate with a relatively sparse pubescence concentrated at the base of the beak (vs. the rather copious and widespread pubescence of *C. deflexa*). The staminate spike of *C. austrodeflexa* is longer and thicker than that of *C. deflexa* (3–9 mm long and 1–2 mm thick vs. 2–5 mm. long and 0.5–1 mm thick), and the staminate scales are also proportionately larger. The length of the lowest pistillate bract in *C. austrodeflexa* is subequal to the staminate spike, although it may vary from shorter than to greatly exceeding the staminate spike (vs. typically exceeding the staminate spike in *C. deflexa*). Finally, the ranges of *C. deflexa* and *C. austrodeflexa* do not overlap. The former is a plant of arctic-boreal and north temperate regions, in the east extending southward to southern New England and disjunctly to the high Appalachians of West Virginia, North Carolina, and Georgia; the latter is confined to the coastal plain from southeastern Virginia to northwestern Florida, southwestern Alabama, and northwestern Louisiana.

Carex austrodeflexa could be confused with two other coastal plain species of section *Acrocystis* that produce basal pistillate spikes, *Carex umbellata* Schkuhr ex Willd. and *Carex tonsa* (Fern.) E.P. Bicknell. They differ by perigynium shape and indument, staminate spike characters, rhizome length, pistillate bracts, and habitat. *Carex austrodeflexa* has elliptic to narrowly obovate perigynia, whereas *C. umbellata* and *C. tonsa* have globose to broadly ovoid perigynia. Perigynia of *C. austrodeflexa* are glabrous to glabrate and with a papillose surface; those of *C. umbellata* are densely puberulent, those of *C. tonsa* sparsely puberulent or sometimes glabrous; neither has a papillose surface. In its distal inflorescences *C. austrodeflexa* always has a staminate spike closely associated with two pistillate spikes, whereas in *C. umbellata* and *C. tonsa* the staminate spike is associated with one pistillate spike or is solitary. *Carex austrodeflexa* differs from *C. umbellata* in its long slender red rhizomes and matted habit (vs. the short reddish to brown rhizomes and distinctively cespitose habit of *C. umbellata*). From *C. tonsa*, *C. austrodeflexa* may be separated by its slender, red-sheathed rhizomes (vs. short, thick rhizomes). The lower pistillate bracts of *C. austrodeflexa* are typically much longer than those of *C. umbellata* and *C. tonsa,* which have bracts usually much shorter than the staminate spike. Both *C. umbellata* and *C. tonsa* inhabit dry to xeric situations, often in full sun, whereas *C. austrodeflexa* grows in wet shaded streamheads and margins of small-stream swamps.

Finally, *Carex austrodeflexa* may be confused with two other members of section *Acrocystis*, *Carex emmonsii* Dewey ex Torr. and *C. floridana* Schweinitz. *Carex austrodeflexa* shares the bright red sheath character with *C. emmonsii*, and the two species occasionally grow together, but they are easily separated by the long-creeping rhizomes and basal pistillate spikes of *C. austrodeflexa*. Some plants of *Carex floridana* produce short fertile culms as well as long ones and thus resemble *C. austrodeflexa*, but the former is a much coarser plant, has leaves twice as wide as those of *C. austrodeflexa*, has longer, much thicker rhizomes forming clonal patches, has perigynia covered with short pubescence but non-papillate (vs. glabrous and papillate), and occupies dry to dry-mesic habitats.

One morphological character deserves special mention: papillose perigynia surfaces. No other species in section *Acrocystis* has this feature so prominent; all others are non-papillate or have small papillae obscured by trichomes (Reznicek *in litt*, Poindexter *in litt*.). Thus, strongly papillose perigynia is a unique character state, and when coupled with its southern coastal plain range, makes *C. austrodeflexa* a highly distinctive species.

KEY TO SOUTHEASTERN COASTAL PLAIN *ACROCYSTIS*

(Adapted from Weakley 2008; Crins & Rettig 2002; Werier 2006)

1. Some spikes borne well above the middle of the culm, and also some pistillate spikes borne on short or elongate peduncles from the base of the culm.
   2. Terminal staminate spike 3–9 mm long, always associated with sessile pistillate spikes; perigynia elliptic or narrowly obovate, surface papillose ____ **Carex austrodeflexa**
   2. Terminal staminate spike 5–15 mm long, solitary or associated with a pistillate spike; perigynia broadly ovate to globose, surface pubescent to glabrous but not papillose.
      3. Perigynia subcoriaceous, 3.5–4.5 mm long, the body very sparsely short-pubescent or glabrous; leaf blades thick, stiff, deep green, spreading at maturity, 2–4.5 mm wide; plants loosely cespitose with short-ascending rhizomes; achenes brownish at maturity, shining, pitted ____ **Carex tonsa**
      3. Perigynia membranaceous, 2.2–3.2 mm long, the body short-pubescent; leaf blades thinnish, not stiff, light green, erect or ascending at maturity, 1.5–3 mm wide; plants densely cespitose; achenes, brownish-black or black at maturity, either minutely pitted or obscurely and irregularly pitted ____ **Carex umbellata**
1. All spikes borne close together well above the middle of the culm; no pistillate spikes borne on separate peduncles from the base of the culm.
   4. Plants with long rhizomes, forming clonal patches.
      5. Achene body mostly 1.5–1.7 mm long; fertile culms 7–17 cm tall, usually much shorter than leaves; pistillate scales mostly 3–3.7 mm long ____ **Carex floridana**
      5. Achene body mostly 1.2–1.3 mm long; fertile culms 20–43 cm tall; equaling or exceeding leaves; pistillate scales mostly 2.6–3 mm long ____ **Carex physorhyncha**
   4. Plants cespitose, not forming clonal patches.
      6. Achene body mostly 1.4–1.6 mm long; fertile culms mostly 2–20 cm tall.
         7. Culm height (4.5–)6.6–38(–51) cm tall, widest leaf (1.9–)2.3–4.5 mm wide ____ **Carex nigromarginata**
         7. Culm height 1.9–9.9(–13.7) cm tall, widest leaf 1.2–2.2(–2.5) mm wide ____ **Carex reznicekii**
      6. Achene body mostly 1.2–1.3 mm long, fertile culms mostly 17–35 cm tall.
         8. Staminate spikes 8.4–11 mm long, scales from median portion of spike with weak midrib not extending to tip ____ **Carex albicans**
         8. Staminate spikes 5–8.4 mm long, scales from median portion of spike with prominent midrib extending to tip or even slightly aristate ____ **Carex emmonsii**

HABITAT, PHENOLOGY

A distinctive feature of *Carex austrodeflexa* is its habitat: it is the only species within section *Acrocystis* in the southeastern United States restricted to wetlands. Moreover, its wetland habitats are embedded within the fire-maintained longleaf pine ecosystem (Christensen 1988; Peet & Allard 1993; Platt 1999). Within areas currently managed with fire, habitats of the new sedge burn every 2–5 years. Without fire, populations may persist for many years (pers. obs.), but precise data are lacking. *Carex austrodeflexa* occurs in two wetland community types. First, it inhabits seepage-fed streamheads (termed baygalls or steepheads in the Gulf Coastal Plain) and their ecotones. These streamheads are forested with *Acer rubrum* L., *Chamaecyparis thyoides* (L.) B.S.P., *Liriodendron tulipifera* L., *Magnolia virginiana* L., *Nyssa biflora* Walt., *Pinus palustris* P. Mill., and *P. serotina* Michx. Shrubs include *Clethra alnifolia* L., *Ilex coriacea* (Pursh) Chapm., *Ilex glabra* (L.) A. Gray, *Lyonia lucida* (Lam.) K. Koch, *Morella caroliniensis* (P. Mill.) Small, and *Toxicodendron vernix* (L.) Kuntze. Vines of *Smilax laurifolia* L. and the coarse grass *Arundinaria tecta* (Walt.) Muhl. also occur. *Sphagnum* (may include *S. palustre* L., *S. affine* Reynauld & Cardot, and *S. tenerum* Sull.) and other mosses are nearly always present, and *C. austrodeflexa* is most abundant within moss patches. Herbaceous associates include *Carex atlantica* Bailey, *C. collinsii* Nutt., *C. lonchocarpa* Willd., *Chasmanthium laxum* (L.) Yates, *Eupatorium pilosum* Walt., *Eurybia paludosa* (Ait.) Nesom, *Rhynchospora cephalantha* A. Gray var. *attenuata* Gale, *R. leptocarpa*

(Chapm. ex Britton) Small, *Sarracenia purpurea* L. var. *venosa* (Raf.) Fern., *Sarracenia rubra* Walt., *Solidago patula* Muhl. ex Willd. var. *strictula* Torr. & A. Gray, and *Xyris platylepis* Chapm.

Second, *Carex austrodeflexa* inhabits non-alluvial swamp forest (also called small-stream swamp forest) and especially their ecotones with wet, grass-sedge-herb savannas. In the outer coastal plain of North Carolina, several populations of *C. austrodeflexa* occur in association with many globally rare and restricted species, such as *Carex lutea* LeBlond, *Parnassia caroliniana* Michx., and *Thalictrum cooleyi* Ahles. Common associates include *Acer rubrum, Carex atlantica, Carex leptalea* Wahlenb., *C. lonchocarpa*, *C. styloflexa* Buckley, *Liriodendron tulipfera, Morella cerifera* (L.) Small, *Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray, and *Taxodium ascendens* Brongn. In this habitat *C. austrodeflexa* may be a patch dominant in the herb layer.

Carex austrodeflexa flowers early, beginning in late February and often peaking in the first two weeks of March in the Sandhills region of the Carolinas and eastern Georgia. It reaches its peak fruiting period in early and mid April. The populations on the outer coastal plain of North Carolina and on the Gulf Coastal Plain reach floral peak one to two weeks earlier than those in the inland portion of its range.

RARITY AND CONSERVATION

Carex austrodeflexa is not a rare plant from a global perspective. In our opinion it is merely overlooked, as from a short distance flowering plants can appear to be merely vegetative and fruiting culms wither rapidly following maturation. In North Carolina new populations are found almost annually without directed searches. We believe that many more populations will be documented in other southeastern states, once botanists learn its morphology and habitat. That said, however, we believe that chances of finding *C. austrodeflexa* increase significantly within areas managed with controlled burns.

ACKNOWLEDGMENTS

The authors wish to thanks curators and staff of the following herbaria for access to specimens: CLEMS, FSU, MICH, NCSC, NCU. Tony Reznicek (MICH) and two reviewers (Theodore S. Cochrane and one anonymous) significantly improved the manuscript. Alan Weakley (NCU) provided guidance and support throughout. Guy Nesom (Fort Worth, Texas) kindly provided the Latin diagnosis.

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BOOK NOTICES

Randall T. Schuh and Andrew V.Z. Brower. 2009. **Biological Systematics: Principles and Applications, Second Edition.** (978-0-8014-4799-0, hbk.). Comstock Publishing Associates, (**Orders:** www.cornell-press.cornell.edu/ordering/; orders@nbninternational.com, CUP Services, Attn: Orders, P.O. Box 6525, 750 Cascadilla Street, Ithaca, New York 14851-6525, U.S.A.). $59.95, 328 pp., 65 illustrations, tables, charts, graphs, maps, b/w line drawings, 6⅛" × 9¼".

I found this textbook to be quite educating; it had, however, a great deal of complex terms that I was not familiar with, though a glossary was provided that made my endeavor much easier. I enjoyed the author's inclusion of bits of history and background information on systematics and nomenclature. The authors summarize and condense the many topics of cladistics while including small but important details. It also mentions the important place of phylogenetic studies inside biological taxonomy. In conclusion I find this to be a very informative textbook for those studying biology. This is hardly a casual read for the rest of us.—*Deanna Callahan, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

MISSOURI BOTANICAL GARDEN PRESS (ST. LOUIS, MISSOURI)

Orchids

Carl A. Luer. 2010. **Icones Pleurothallidinarum XXXI: *Lepanthes* of Bolivia. Systematics of *Octomeria*. Species North and West of Brazil (Addenda: New species of *Brachionidium, Lepanthes, Masdevallia, Octomeria, Platysele, Pleurothallopsis,* and *Porroglossum*. Corrigenda).** (ISBN 978-935641-00-1, pbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 120. Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $65.00, 154 pp., illus., 7" × 10".

BOOK REVIEW

Elray S. Nixon, with illustrations by Bruce Lyndon Cunningham. 2010. **Gymnosperms of the United States and Canada.** (9780934115032, hbk.; 9780934115056, pbk.). Bryce Lyndon Cunningham Productions 180 County Road 8201, Nacogdoches, Texas 75964, U.S.A. (**Orders:** www.artplantaebooks.com/). $70.00 (hbk.), $59.95 (pbk.), 208 pp., color illustrations, 8½" × 11".

Professor Emeritus Nixon and Artist Cunningham have definitely teamed up to produce an outstandingly beautiful and helpful flora of the gymnosperms of the United States and Canada. As Professor Cunningham notes in his preface, "This book is intended for beginners in dendrology and plant taxonomy and others who are interested in the gymnosperms of North America."

Anyone who spots the volume, either online or in a bookstore, will be immediately drawn to the beautifully illustrated cover—and then equally delighted to find that author and artist cooperated throughout the entire volume to provide exquisitely accurate artwork and specific information at every level of the gymnosperms. The first ten pages provide introduction, plant classifications, plant names, keys, identification aids, and distribution maps. Page 11 has a succinct, straightforward Key to Divisions. Following pages include keys to families, to genera, and to species. The accompanying illustrations make it very easy to identify specific parts and to see the differences being described.

Also very helpful is the Illustrated Glossary, beginning on p. 166. This is followed by a page of references (p. 178) and then an Index of Vernacular (Common) names, starting on p. 179.

Unexpected, but of interest, are pp. 182 to 199. These have illustrations of various diverse and intriguing items (based on materials in the volume) that are for sale. Page 200 heralds an upcoming publication and a dedication and tribute to a colleague.

This volume is particularly helpful for nature lovers and people who really enjoy the Great Outdoors. The straightforward keys and descriptions, accompanied by the illustrations, are bound to captivate the reader.—*Helen Jeude, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

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PHASEOLUS HYGROPHILUS (LEGUMINOSAE-PAPILIONOIDEAE), A NEW WILD BEAN SPECIES FROM THE WET FORESTS OF COSTA RICA, WITH NOTES ABOUT SECTION *BREVILEGUMENI*

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ABSTRACT

A new pluriannual species of *Phaseolus* has been found on the Pacific slope of central Costa Rica, in an intact wet forest of the San José province. It could belong to the section *Brevilegumeni* of the genus, and differs from *P. oligospermus* by the round based leaflets with central permanent variegation, multi-flowered pseudoracemes with cup-shaped round primary bracts, flowers with white wings and light pinkish standard, slightly falcate pods with three lentil-like seeds. Its ecological niche is wetter and with a shorter dry season as compared to that of the latter species. Only two populations of the new taxon are known to date in this part of Costa Rica.

RESUMEN

Una nueva especie plurianual de *Phaseolus* ha sido encontrada en la vertiente pacífica central de Costa Rica, en un bosque intacto lluvioso de la provincia de San José. Podría pertenecer a la sección *Brevilegumeni* del género, y se diferencia de *P. oligospermus* por sus foliolos no lobulados con base redonda, variegación central permanente, seudoracimos multiflores con brácteas primarias redondas encorvadas, flores con alas blancas y estandarte rosado muy claro, vainas ligeramente falcadas con tres semillas lenticulares. Su hábitat es más lluvioso y con una estación seca más corta en comparación a este último taxón. Se conocen a la fecha dos poblaciones de la nueva especie en este sector de Costa Rica.

INTRODUCTION

In an attempt to locate all populations of wild common bean, *Phaseolus vulgaris* L., in Costa Rica (as part of the project "Gene Flow Analysis for Environmental Safety in the Neotropics"), two of the authors (DGD and RAV) entered in December 2003 in the watershed of Río Savegre (central southern part of that country), through a dirt path from the hamlet División westwards to get back to the Cantón de Dota, and found a bean species new to science. Early observations in the field at the original collection site and during cultivation in Colombia indicate that it could belong to section *Brevilegumeni* Freytag (Freytag & Debouck 2002). We hereafter present the description of this new taxon, its traits contrasting with those of related species of the section, namely *P. oligospermus* Piper (the type of which is from central Costa Rica; Piper 1926), and information about its ecology.

RESULTS

Morphological observations

The following observations were made on plants growing freely for six years in the field at CIAT experimental station in Popayán, Cauca, Colombia (1,730 masl, 2°30'N, 76°34'W, Andean inceptisol soil) from seeds collected at the type locality in February 2004.

Phaseolus hygrophilus Debouck, sp. nov. (**Figs. 1–6**). Type: COSTA RICA. San José: San Isidro El General, Santa Eduviges, on path to Santa Eduviges 8.8 km from intersection at Divisiόn with Interamerican Highway, Long. 83°45'W, Lat. 9°30'N, alt. 1,520 masl, 11 Dec 2003 (and again on 19 Jan 2006), *DG Debouck & R Araya Villalobos 3172* (holotype: INB; isotypes: BRIT, CR, F, FI, G, GH, INB 0004026793, K, MEXU, MICH, NY, P, UC, USJ 88810; in addition, small amounts of seeds, accessioned as G40815, can be obtained from the Genetic Resources Program of CIAT).

Haec species *Phaseolo oligospermo* similis, sed ab eo foliolis non lobulatis ad centrum variegatis, inflorescentiae bracteis primariis cupulatis, bracteolis rotundatis mayoribus alisque albidis cum vexillo subroseo distinguitur. Crescit in sylvis pluvialis montium declivitatis Pacificae Costa Ricae ad 1,500 m supra mare rarus.

Plant a pluriannual, mid-sized, indeterminate vine to 4–6 m long with 8–16 lateral inflorescences (Fig. 1). **Seedling** 7–8 cm high, from hypogeal germination, epicotyle green with some red (147A)[1] spots, terete, 30–40 mm long, sparsely covered with minute uncinate hairs. Eophylls petiolate, opposite, 27 × 18 mm, dark green (144A) with variegation along the midvein, covered with minute uncinate hairs, the blade acuminate, base somewhat rounded, the petioles green, canaliculate, 15–18 mm long, the pulvini markedly reddish, the stipules 2 mm long, triangular purplish (59A) 4-nerved. First true leaf trifoliolate (Fig. 1b). **Root** herbaceous, fibrous, up to 60–80 cm long, tan yellowish brown (22C), much branched at the beginning of growth (Fig. 1a), the 4–6 main lateral roots becoming tuberous during the second and subsequent years. Adventitious roots produced at lower nodes of stems (Fig. 2c), after months becoming tuberous, 8–15 cm long, fusiform pyriform. **Stems** terete, green (147D), exposed parts turning reddish in sunlight, the nodes purplish (60B), internodes 9.5–13.4 cm covered with uncinate trichomes; sprawling horizontally from the lower nodes of the main stem, rooting with help of adventitious roots, climbing and twining from the upper nodes of main stem; usually 2–4 shoots in the lower part of the plant, 2–4 shoots in the upper part. Stipules green (141C) triangular lanceolate basifix multiveined 5 × 3 mm. **Leaves** trifoliolate, dark green (136A) with bluish tone, membranaceous, lustrous, with a clear variegation (138C) along central veins (still apparent on dry herbarium vouchers) (Fig. 1d), covered with uncinate trichomes more abundant on the inner surface as compared to the upper side. Leaflets lanceolate apiculate, the terminal leaflets with a more acute apex as compared to the lateral ones, the base rounded. Terminal leaflet 7.7(–13.1) × 5.0(–8.0) cm. Lateral leaflet 5.3(–10.8) × 3.3(–7.1) cm. No lobation observed. Petiole terete, canaliculate, green 3.3–8.5 cm. Foliar rachis terete, green, 1.2–2.8 cm. Proximal pulvini purplish (77A), conspicuous. Distal pulvini green (136B). Stipels green (138B), linear, narrowly triangular, 2–3 × 1–1.5 mm, two at the base of the pulvinus of the terminal leaflet, one subtending the pulvinus of each lateral leaflet. **Inflorescence** a pseudoraceme (Fig. 1c, 1e; Fig. 2b), appearing as a greenish white (145B) axillary spherical mass at the beginning of floral development. Peduncle 40–50 mm long, terete, scandent, curved in lower part, erect in upper part, almost glabrous with sparsely distributed minute uncinate hairs, light green (143B). Rachis erect, terete, twice as long as the peduncle, 70–120 mm long, light green (143A). Number of primary bracts subtending the secondary racemes: 9–16 or more. Primary bracts 5 × 5 mm, rounded, cupped, multi(8–10)nerved, light green (145D) with many brick reddish dots (79D), sometimes caducous after anthesis. Pedicels terete, glabrous, light green, 12–16 mm to 20 mm with maturing pod. Pedicelar bracts rounded, cupped, 2.5 × 2 mm. **Flowers** papilionaceous (Fig. 1f, 1g; Fig. 2d) white sometimes with standard light pink, two for each secondary raceme (Fig. 2b). Bracteoles (Fig. 1i) pale light green (149C), ovate cordiform, 3.5 × 3 mm, 6-veined, a few veins purplish (79D). Calyx round, glabrous, cupped (Fig. 1h), green turning tan at insertion of pedicel when pod matures; tube 3.5 mm long, greenish (142D) with minute reddish dots (79D); lobes conspicuous, convex (prominent during early ontogeny of floral buds), two upper lobes rounded 4 × 4 mm, three lower lobes rounded apiculate 3 × 3 mm narrowing to 2 mm at insertion on the tube. Corolla fading cream yellow (13A–C) on the day after anthesis. Standard (Fig. 1j) outer face whitish glabrous with light purple (75B) dots at flexure, inner face white sometimes with a pink (75D) cast towards the upper half and left auricle, broadly rectangular with sinus 3 mm deep, length from insertion to flexure 9 mm and from flexure to upper margin 12.5 mm, strong and 12 mm at flexure, width 14 mm; asymmetrical with left auricle 6 mm wide right auricle 8 mm wide, left auricle with margin

[1]Parenthetical codes after colors are taken from Anonymous 1966.

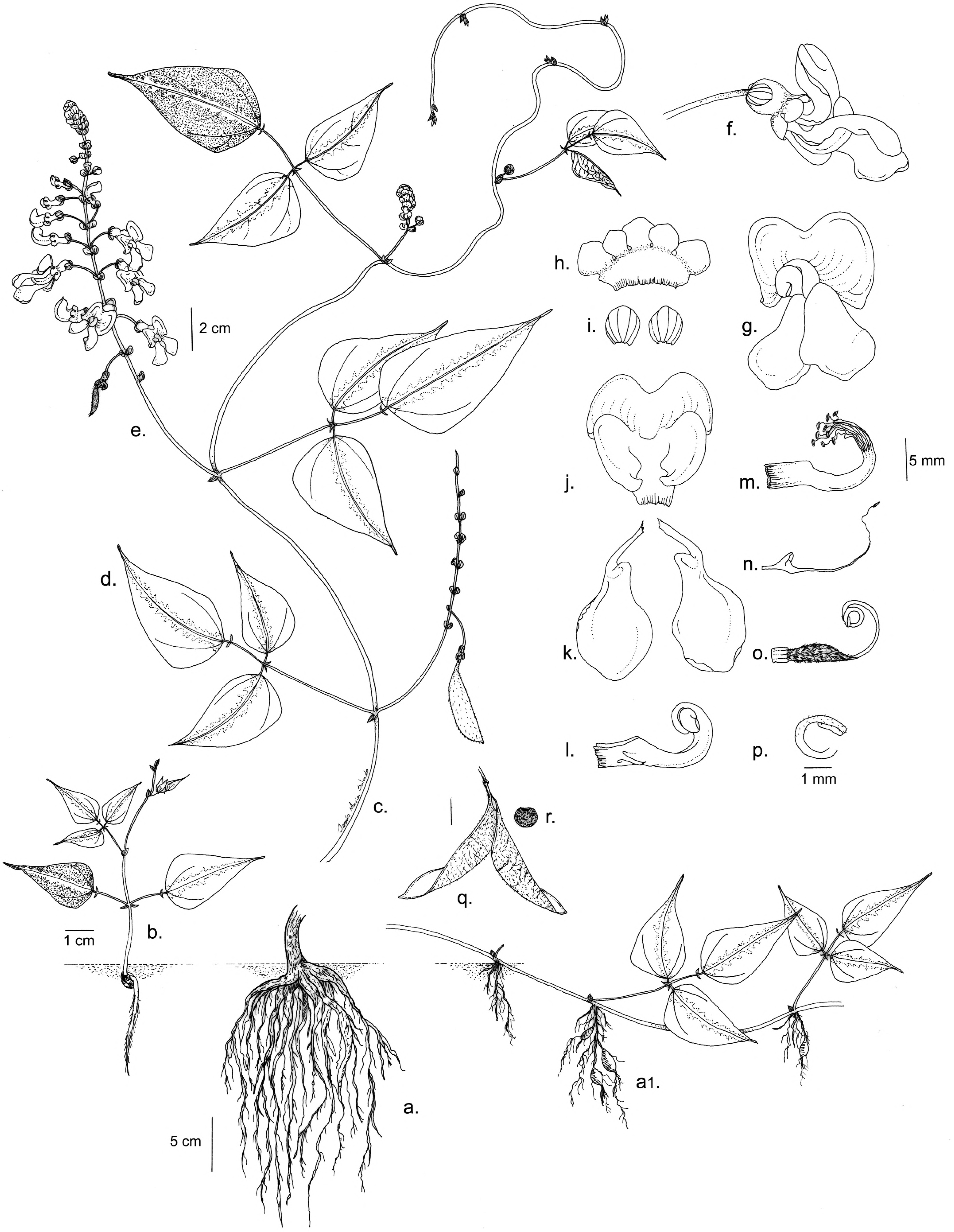

Fig. 1. Drawing of *P. hygrophilus* with all its parts. a: root. b: seedling. c: flowering stem. d: trifoliolate leaf. e: pseudoraceme. f: flower, lateral view. g: flower, front view. h: calyx. i: bracteoles. j: standard. k: wings. l: keel. m: staminal tube. n: vexillary stamen. o: ovary and style. p: stigma. q: pod. r: seed.

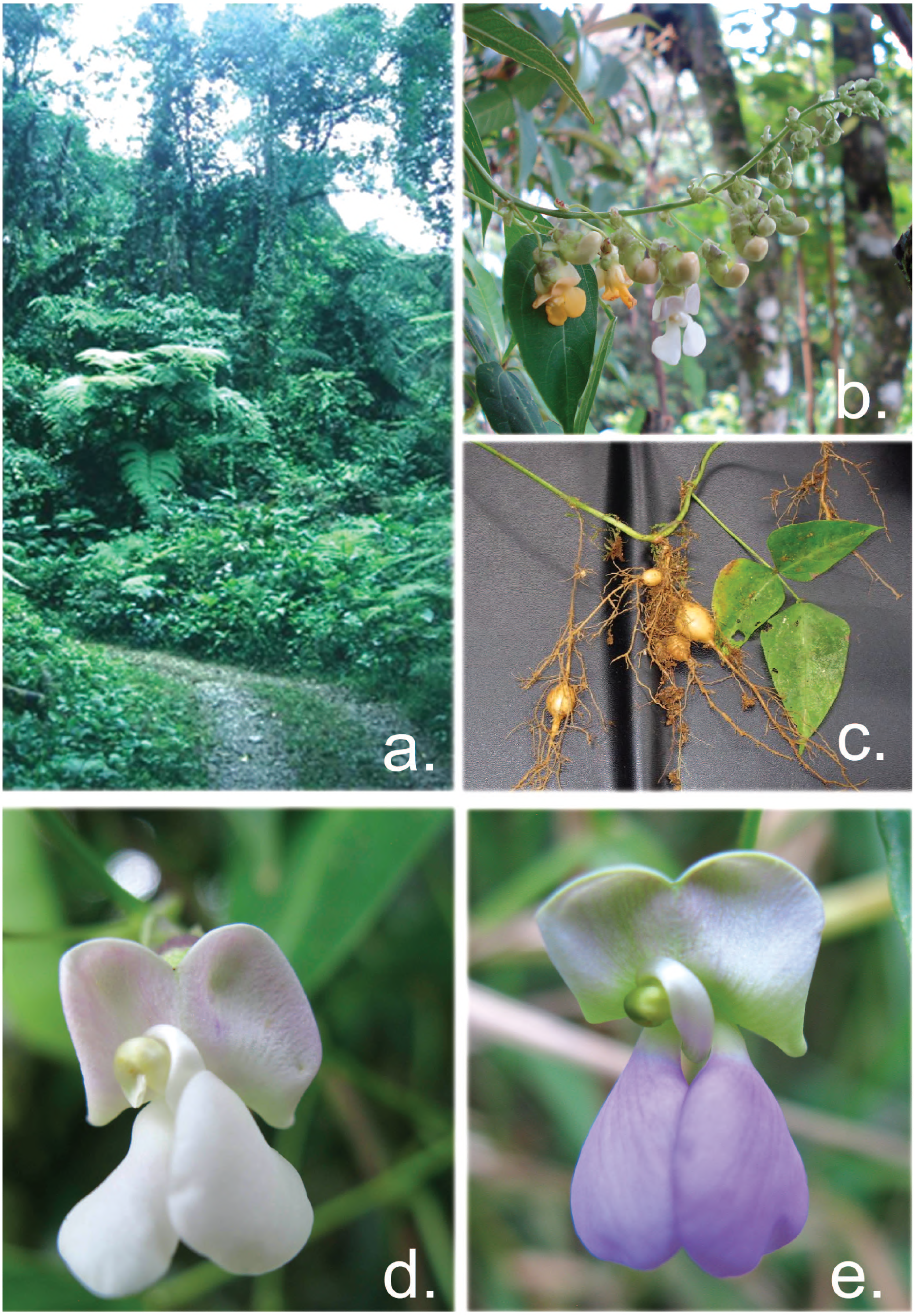

Fig. 2. **a:** habitat of *P. hygrophilus*. Note the presence of tree ferns. **b:** close-up of pseudoraceme at flowering. **c:** close-up of adventitious root system. **d:** close-up of flower of *P. hygrophilus* (DGD-3172). **e:** close-up of flower of *P. oligospermus* (X-16694) (photographs a, c taken at the collection site of *DG Debouck & R Araya Villalobos 3172*; b, d and e taken at CIAT Popayán station in Colombia).

much reflexed; claw whitish with prominent parallel callosities. Wings (Fig. 1k) pure white, glabrous, spreading obtusely, left wing 20 × 9 mm, right wing 20 × 10 mm, rounded obovate; margins not revolute but right wing often superseding on the left one; spur rounded adhering to the keel; claws linear 6 mm long. Keel tubular (Fig. 1l) white greenish at insertion, asymmetrical with two close coils in the terminal part counterclockwise (facing the keel) with a diameter of 4 mm, the final coil smaller with a diameter of 3 mm, the two petals joined all along, ca 14 mm long, 3 mm wide up to the non prominent pockets adhering to the wings, 2 mm wide at the tube, tube 4 mm long to the coils. Stamens diadelphous (9+1), staminal tube (Fig. 1m) 12 mm long delicately veined, vexillary stamen (Fig. 1n) 15 mm long, claw terete 2 mm long with rounded cupped knob diameter 2.5 mm, anthers oval dithecal dorsifixed. Ovary (Fig. 1o) light greenish, heavily pubescent, laterally compressed, 7.5 mm long, 2 mm wide, with 4–5 ovules inserted on a delicately veined basal disk 2 mm long. Style (Fig. 1o) 12 mm long, coiled with 1.5 close coil at the tip, terete, glabrous but with a loose brush of sparsely distributed hairs below and along the stigma; stigma (Fig. 1p) internal narrowly triangular 1 mm long, not extending beyond the tip of the style. **Pollen** (Fig. 4a, 4d) triporate, spherical, diameter 40 microns, exine finely reticulate, tectum finely punctate. **Pods** laterally compressed (Fig. 1q), usually 3-seeded, rarely 2 or 4-seeded, when mature 52–64 mm long and 9–13 mm wide, green (145A) turning dark tan or brown at maturity, with sparsely (densely on 4–5 days old pods) distributed pubescence of straight coffee brown hairs 0.8 mm long. Upper suture rectilinear, lower suture curved boat shaped. Base of pod stipitate, narrow, 1.5–2 mm diameter. Beak right, short, 1.5–3 mm long. **Seeds** circular and lenticular (Fig. 1r; Fig. 3a) 6 mm long, 6 mm wide, 2 mm thick, 6.4 g/ 100 seed, grey (199A) with fine black spots at higher density around the hilum, shiny.

Etymology.—The epithet has been chosen because of the wet habitat in which the population # 3172 has been found (Fig. 2a). According to local informants just outside the ranch of Santa Eduviges about 1 km from the type collection site, the dry season lasts only about 6–8 weeks in the period April–May.

Geographic distribution, ecology and conservation status.—*Phaseolus hygrophilus* seems to be the first bean species found in wet/ rain forests with frequent mist, among tree ferns, many climbing lianas and epiphytes (Fig. 2a). The original location would correspond through the geographic coordinates to the Bp-P or Bp-MB (for 'Bosque pluvial premontano' and 'Bosque pluvial montano bajo', or lower montane rain/ wet forest, according to Tosi 1969; Bolaños & Watson 1993, or Gargiullo 2008). According to Herrera-Soto and Gómez-Pignataro (1993), the type locality would be at the limit of biotic unit 24 (Fig. 5), which corresponds to temperate tropical cool wet habitat with a dry season of 3–4 months. Associated plants are typical of humid habitats with often thin broad leaves, and belong to the families: Acanthaceae, Balsaminaceae, Begoniaceae, Bromeliaceae, Dioscoreaceae, Heliconiaceae, Melastomataceae, Passifloraceae, and Piperaceae. It grows in the understory of natural openings and on path sides, with stems sprawling on the ground first and then climbing before flowering. The new species seems to be rare, known from only two sites on the southern slope of Cerro Buena Vista, extending over an area of 20–30 km^2 (Fig. 5). The two sites from which it has been reported are on the southeastern border of the Reserva Forestal Los Santos. At the time of our visits in 2003 and 2004 there was little disturbance inside this part of the Reserva but severe deforestation around Santa Eduviges confirming observations by Sánchez-Azofeifa and co-workers (2003) about forest cover loss in 10 km-buffer zones of protected areas. We have so far not found *P. hygrophilus* with any other *Phaseolus* species, although it might be at the limit of the range of *P. tuerckheimii* Donnell-Smith (Fig. 6).

Paratype: **COSTA RICA. San José:** San Isidro El General, Las Nubes, 4.4 km SW from Santa Eduviges on dirt road to San Isidro, Long. 83°46'W, Lat. 9°28'N, alt. 1,570 masl, 11 Dec 2003 (and again on 19 Jan 2006), *DG Debouck & R Araya Villalobos 3173* (CR, USJ 88827).

Morphology and possible species relationships in section Brevilegumeni.—The overall morphology of *P. hygrophilus* suggests a relationship with *P. oligospermus*, namely the size of the plant, the ferruginous and abundant pubescence, shape and size of pods, the size and morphology of flowers and seeds. At first glance an outstanding feature of this species is the clear variegation on all leaflets (Fig. 1c). Variegation is often present along the main vein of terminal leaflets of *P. oligospermus*, while very well marked and apparently constant on all leaflets in *P. hygrophilus*. Leaflet variegation seems only matched by that of *P. pedicellatus* Benth.,

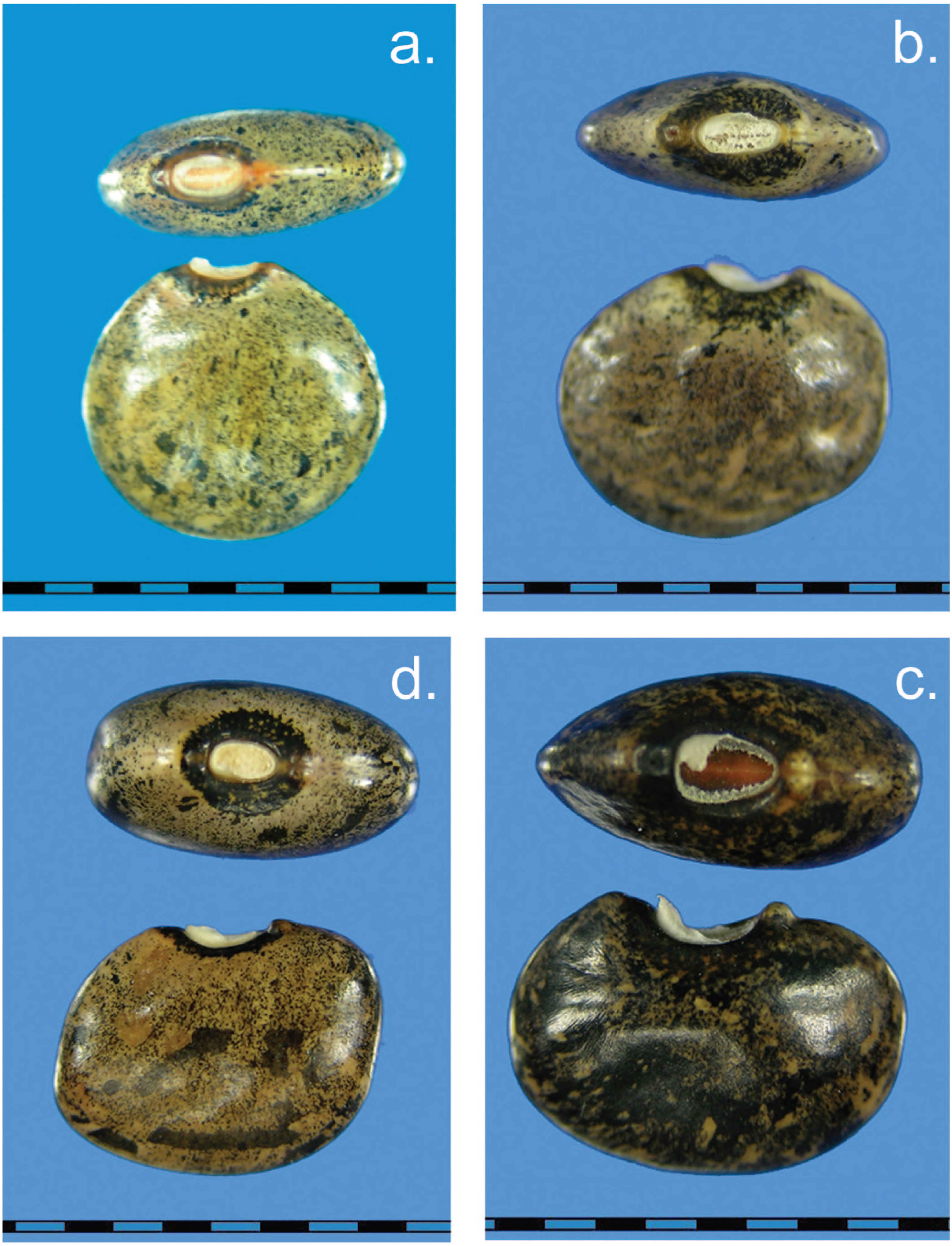

Fig. 3. Close-ups of seeds, scales at bottom in mm. Clockwise: a: *P. hygrophilus* (DGD-3172; INB, F, GH). **b:** *P. oligospermus* (DGD-2091; CR). **c:** *P. tuerckheimii* (DGD-1617; BR, K, MICH, SI, US). **d:** *P. vulgaris* (DGD-3168; INB).

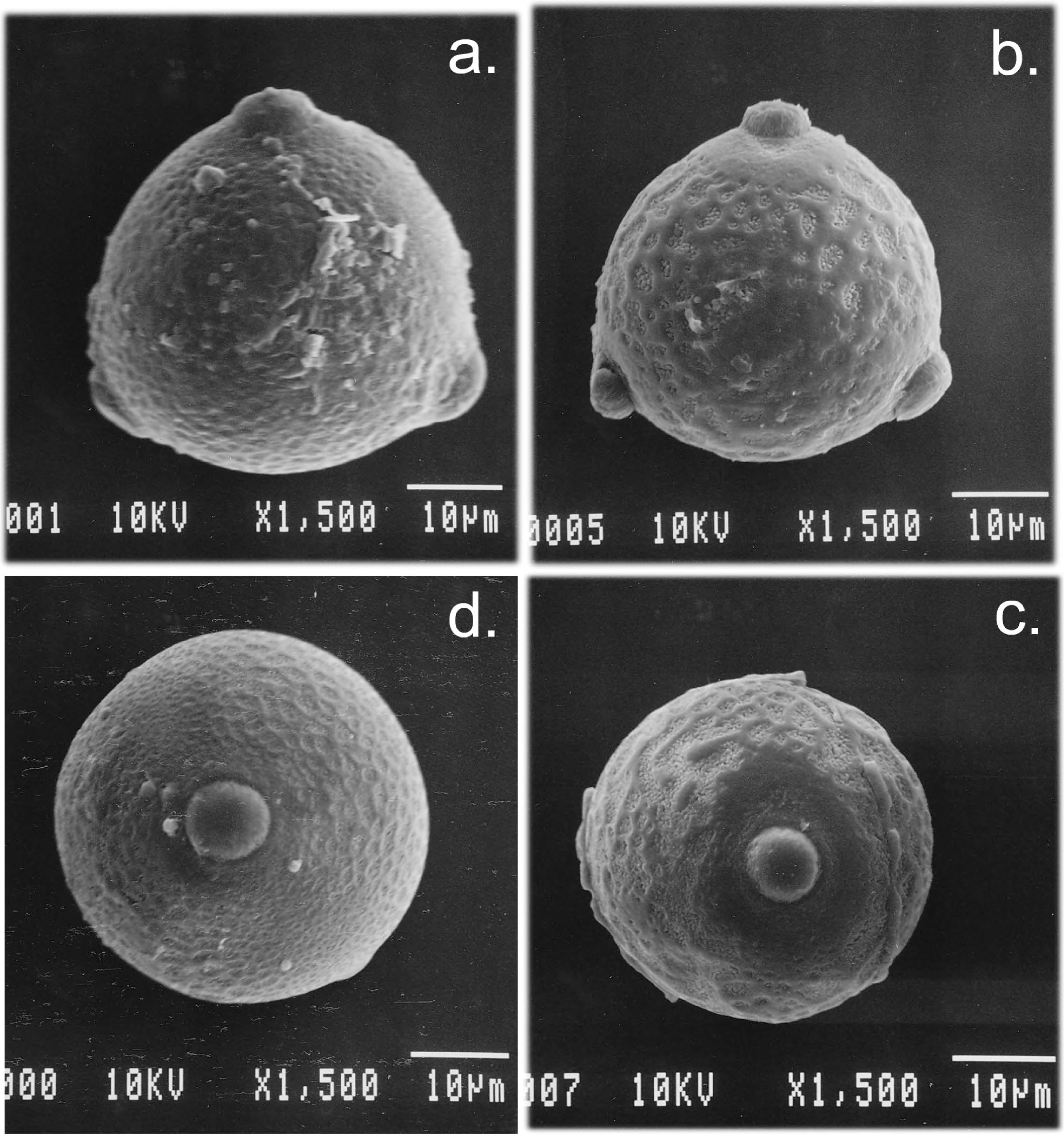

Fig. 4. Pollen of *P. hygrophilus* (left: a and d, clockwise; DGD-3172) and of *P. oligospermus* (right: b and c; X-16694). Upper row: polar views (4a, 4b); lower row: equatorial views (4c, 4d).

although the color of the leaflets is less intense in the latter (Freytag & Debouck 2002). The variegation, which can still be seen on some voucher specimens, is so striking in *P. hygrophilus* that it could be of ornamental value. The base of terminal leaflets is often cuneate in *P. oligospermus*, and that of lateral leaflets slightly or clearly lobed (Freytag & Debouck 2002; Zamora 2010), while the base of all leaflets is smoothly rounded in *P. hygrophilus*. In both species, leaflets are membranaceous, but shrivel very quickly upon drying in *P. hygrophilus*, because of the humid habitat. Tuberous roots are usually cylindrical-conical in *P. oligospermus*, and spherical-fusiform in *P. hygrophilus*; adventitious roots can appear at lower nodes of lateral stems when they spread onto the mulch, and later become tuberous (Fig. 2c). These lateral shoots eventually flower, while the original main stem may lose vigor and die. Wings and standard are pure white often with a pinkish

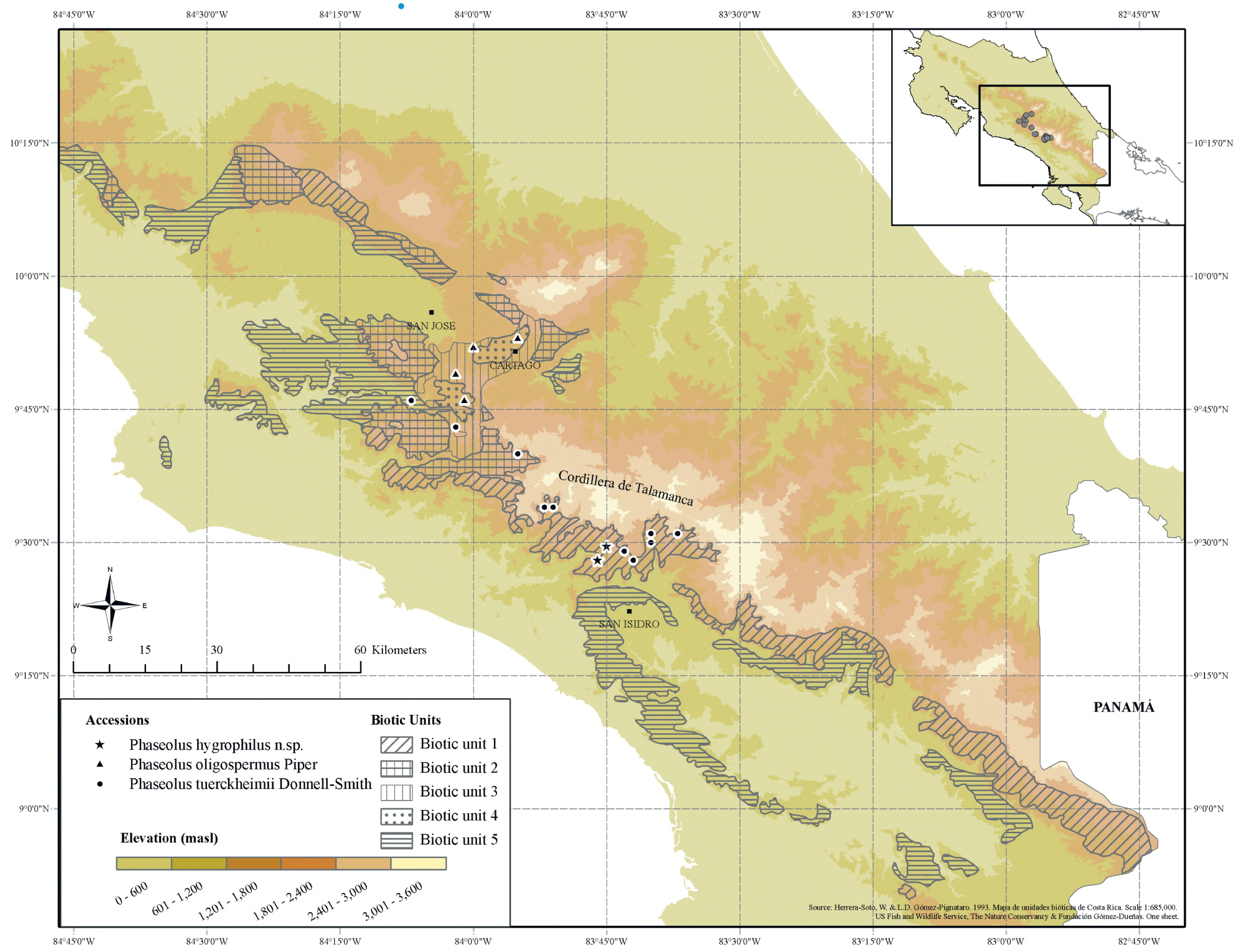

Fig. 5. Distribution map of *P. hygrophilus, P. oligospermus* and *P. tuerckheimii* in central eastern Costa Rica. Inlay map: location of the study area. Base map with six elevation ranges of 600 m each. Biotic unit 1: premontane rain/ wet with 3–4 dry months; biotic unit 2: premontane moist with 3–4 dry months; biotic unit 3: premontane humid with 3–4 dry months; biotic unit 4: premontane subhumid with 3–4 dry months; biotic unit 5: lower montane humid with 3–4 dry months.

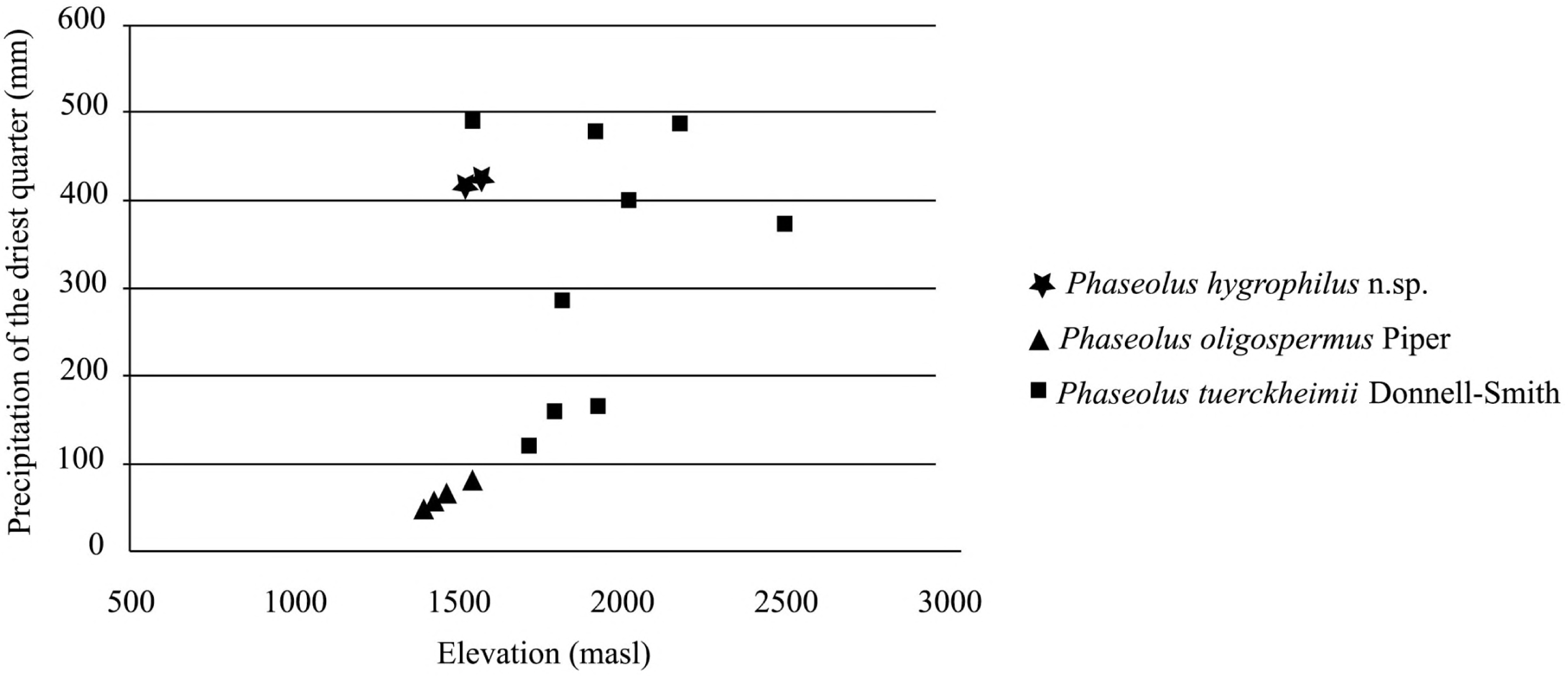

Fig. 6. Distribution of the different populations known from Costa Rica for the three species of *Brevilegumeni*, against altitude of the collection sites and amount of rainfall during the driest trimester of the year.

cast in the front upper part of the standard in *P. hygrophilus* (Fig. 2d), and lilac-purple and greenish, in *P. oligospermus* (Fig. 2e), respectively. Primary bracts are glabrous, rounded and cupped, often caducous, light green with reddish dots in *P. hygrophilus* (the same color pattern being found also in bracteoles and calyx), while they are pubescent, triangular lanceolate persistent, rusty green in *P. oligospermus*. In the latter species, bracteoles are small, triangular, one-nerved, and persistent, whereas in the former they are rounded, indistinctly multinerved, and caducous. Flowers and pedicels are brittle in *P. hygrophilus*, and one can find pseudoracemes without flowers and pedicels, or with pedicels hanging to the rachis while flowers have fallen apart. Another outstanding feature of *P. hygrophilus* is the early and prominent development of calyx lobes giving a crown aspect to the floral bud. The slow floral ontogeny and fruit development (up to two months in the Popayán conditions) as compared to that of *P. oligospermus* (one month, same conditions) is also notable.

On the basis of the above characteristics, and pending molecular analysis, we tentatively locate *P. hygrophilus* in section *Brevilegumeni*. The key to species of that section in the monograph (Freytag & Debouck 2002, p. 220) can be amended as follows.

1. Plants usually 2–6 m, rarely more, strong vines; roots tuberous, not more than 30 cm long. Leaflets lanceolate to truncate asymmetrical, membranaceous, often variegated, sparsely pubescent on both surfaces. Inflorescences large up to 20 cm long with 9–15 insertions of secondary racemes sparsely distributed. Bracteoles variously shaped, noticeable. Flowers white, pink or lilac lavender not bluish violet. Pod straight on upper suture, falcate on lower suture, 3–5 seeded, seed lenticular; pod beak strong up to 5 mm long and variously recurved. Various abundances, geographic ranges (from W Mexico to central Costa Rica), 700–2000 m elevation.
   2. Bracteoles lanceolate, 1–2 mm long. Primary bracts triangular aciculate, 2–4 mm long. Flowers pink or purple. Fruits 4 or 5 seeded. Rare, in S Nayarit and W Jalisco in Mexico, 1300–1400 m elevation ________ **L.1. P. campanulatus**
   2. Bracteoles lanceolate or rounded ovate, 2–5 mm long. Primary bracts lanceolate or rounded, 4–6 mm. Flowers white with parts pink or lilac with parts green. Fruits 2–4 seeded.
      3. Bracteoles lanceolate, 2 mm long. Primary bracts narrowly lanceolate, persisting, 5–6 mm long. Flowers lilac (standard greenish). Leaflets often variegated, the terminal one cuneate at base, the lateral ones often with a rounded lobe. Scarce, from Chiapas in Mexico (through Guatemala, Honduras, Nicaragua) to Cartago in Costa Rica, 700–2000 m elevation ________ **L.2. P. oligospermus**
      3. Bracteoles rounded ovate, 4–5 mm long. Primary bracts rounded cupped, often caducous, 5 mm long. Flowers white (standard white, often light pink on inner face). Leaflets strongly variegated, the terminal one rounded or deltoid at base, the lateral ones rounded at base and none lobed. Rare, central Pacific Costa Rica, 1500–1600 m elevation ________ **L. 3. P. hygrophilus**

1. Plants usually 4–12 m, stout lianas; roots thickened but fibrous, more than 50 cm long. Leaflets ovate, the lateral ones slightly asymmetrical, all nearly coriaceous, not variegated, densely pubescent like velvet. Inflorescences very large up to 30 cm long with more than 15 insertions of secondary racemes (often 20–30) densely distributed towards the apex. Bracteoles reduced to minute scales. Flowers bluish violet (often dark blue in herbarium specimens), rarely white. Pods inflate, straight on upper suture, falcate on lower suture, 2–4 seeded, seed oblong with hilar depression; pod beak stout up to 5 mm long straight or slightly recurved. Scarce, from Chiapas, Mexico (through Guatemala, Honduras, and Costa Rica) to Chiriquí in Panama, above 1400 m elevation ________ **L. 4. P. tuerckheimii**

The geographic distribution from north southwards across Central America has been compiled based on the following voucher specimens (Debouck 2010b) (types underlined).

P. campanulatus (4)

MEXICO. Jalisco: *A Delgado 1180* (CHAPA, MEXU, TEX); *JAS Magallanes 1961* (MEXU). **Nayarit:** *R McVaugh 16341* (MICH), *O Téllez 9346* (IBUG, MEXU).

P. oligospermus (54)

MEXICO. Chiapas: *Arias 844* (CHAPA); *Arias 962* (CHAPA); *Breedlove & Raven 13246* (CAS, F, LL, MEXU, MICH, US); *Breedlove 48132* (CAS, MEXU); *Breedlove 48191* (CAS, MEXU); *Breedlove 53068* (CAS, MEXU, NY); *Breedlove 53246* (CAS, MEXU, MO, NY); *Breedlove 53275* (CAS, MEXU); *Delgado, García, Hernández, Magallanes & Arias 842* (CHAPA, F, GH, MEXU, MICH, TEX); *Freytag & Vakili 78-Mex-74* (BR, F, GH, IBUG, K, MEXU, MICH, MO, NA, UC, US, WIS); *Hernández X-16694* (COL, IEB); *Sousa, Basurto & Ramamorthy 11359* (BM, CAS, MEXU, MO); *Sousa, Basurto & Ramamorthy 11374* (BM, CAS, MEXU, MO); *Téllez 4592* (MEXU); *Ton 3498* (DS); *Ton 3533* (CAS, MEXU, MICH). **Oaxaca:** *Hernández 625* (CHAPA), *Pérez García 2002* (MEXU), *Pérez García 2258* (MEXU), *Torres 10589* (IBUG). **GUATEMALA. Guatemala:** *Debouck & Soto 2472* (AGUAT, BR, COL, M, MICH, SI, US); *Morales 1128* (AGUAT, F). **Jutiapa:** *Freytag & Vakili 78-Guat-18* (BR, GH, MEXU, MO, UC, US). **Zacapa:** *Steyermark 42412* (F, UC). **HONDURAS. Copán:** *Molina 33632* (MEXU). **El Paraíso:** *Nelson & Romero 4290* (MEXU, MO, US). **Francisco Morazán:** *Bustillo 189* (MEXU, MO); *Linares 6520* (MEXU); *Molina 707* (F); *Molina 18658* (F); *Molina 18680* (F); *Molina 31854* (F); *Williams 18533* (GH). **Lempira:** *Molina 12908* (F, US). **Ocotepeque:** *Molina 22147* (F, MO, NY). **EL SALVADOR. Santa Ana:** *Linares & Martínez 1080* (MEXU). **NICARAGUA. Estelí:** Debouck, Araya & Herrera 3208 (HNMN, O); Debouck, Araya & Herrera 3215 (HNMN, O); Grijalva 660 (MEXU); Moreno 12627 (MEXU); Moreno 17903 (MEXU); Moreno 19370 (MEXU, MO); Stevens 10723 (HNMN, MEXU, MO). **Jinotega:** Martínez 1833 (MEXU); Molina 22924 (BM, CAS, F, G). **Madríz:** Debouck, Araya & Herrera 3203 (HNMN, O); Debouck, Araya & Herrera 3206 (HNMN, O); Stevens 16119 (BM, CAS, CR, HNMN, MEXU); Williams 20259 (F, US). **COSTA RICA. Cartago:** *Debouck & Araya 2091* (BR, CR); *Debouck & Araya 3166* (CR); *Debouck & Araya 3179* (CR); *Oersted 30* (K). **San José:** *Debouck, Araya, González & Camacho 3107* (CR).

P. tuerckheimii (66)

MEXICO. Chiapas: *Bachem & Rojas 398* (CHAPA, MEXU); *Breedlove & Raven 8188* (DS, F, US); *Breedlove 23205* (CHAPA, DS, ENCB, F, MEXU, MICH, MO, TEX); *Breedlove 31916* (DS, MEXU, TEX); *Breedlove 41672* (DS, MEXU, MO, TEX); *Breedlove 42582* (DS); *Breedlove 42717* (DS, MEXU, TEX); *Breedlove 48849* (CAS, MEXU, MO, TEX); *Breedlove 49658* (MEXU); *Breedlove 53246* (MEXU); *Breedlove & Bartholomew 55795* (CAS, ENCB, LL, MEXU, MO, TEX); *Machuca 99* (MEXU); *Marin 36* (RSA); *Martínez & Kearns 19294* (MEXU); *Martínez, Márquez, Urquijo & Ramírez* 19752 (MEXU, MO); *Matuda 5522* (LL); *Matuda 6098* (LL, MEXU, US); *Matuda 15522* (MEXU, US); *Ton 2093* (DS, F, LL, MEXU, MO, US); *Ton 5078* (AGUAT, CAS, MEXU); *Ton 5307* (ENCB, G, IBUG, MEXU, MO); *Ton 7299* (CAS, ENCB, K, MEXU, MO); *Zuill 754* (DS, MO). **GUATEMALA. Alta Verapaz:** *von Türckheim 1536* (BR). **Chimaltenango:** *Debouck & Soto 1624* (BR, COL, K, MICH, SI, UC, US). **El Progreso:** *Debouck & Vásquez 2418* (AGUAT, COL, M); *Steyermark 42471* (F). **El Quiché:** *Molina & Molina 30282* (CHAPA, F, MO); *Sharp 45191* (F, MEXU); *Standley 62387* (F). **Guatemala:** *Debouck & Soto 2473* (AGUAT, BR, MICH, SI, US); *Debouck & Soto 2474* (AGUAT, MICH, US). **Huehuetenango:** *Williams, Molina & Williams 22323* (F, GH, US). **Jalapa:** *Steyermark 32551* (F). **Quezaltenango:** *Debouck, Azurdia & Martínez 3085* (AGUAT). **Sacatepéquez:** *Debouck & Soto 1617* (BR, K, MICH, SI, US); *Standley 59991* (F); *Standley 61137* (F); *Véliz 14771* (MEXU); *Véliz 14862* (MEXU). **Sololá:** *Debouck & Azurdia 3097* (AGUAT). **Zacapa:** *Steyermark 42471* (F). **HONDURAS. El Paraíso:** *Linares 6443* (MEXU). **Francisco Morazán:** *Molina & Molina 21483* (BM, DS, ENCB, F, GH, ITIC, LL, UC, US); *Williams, Molina & Merrill 15597* (F). **Ocotepeque:** *Nelson 4044* (MEXU). **COSTA RICA. San José:** *Burger 4028* (BM, CR, F, MO, US); *Debouck & Araya 2110* (CR, US, USJ); *Debouck, Araya, Ocampo & González 2125* (BR, CR, K, MICH, US, USJ); *Debouck, Araya, Ocampo & González 2129* (BR, CR, K, US, USJ); *Debouck, Araya, Ocampo & González 2131* (BR, COL, CR, K, MICH, SI, UC, US, USJ); *Debouck, Araya, Ocampo & González 2133* (CR, K, MICH, US, USJ); *Debouck, Araya, Ocampo & González 2134* (CR, K, MICH, UC, US, USJ); *Debouck, Araya, González & Camacho 3110* (CR, USJ); *Debouck & Araya 3171* (CR); *Debouck & Araya 3183* (CR); *Williams, Jiménez & Williams 24362* (F). **PANAMA. Chiriquí:** *D'Arcy 9777* (MO); *D'Arcy 9881* (MEXU, MO); *Davidse & D'Arcy 10145* (MEXU, MO); *Davidson 927* (A); *Davidson 948* (A, F, MO, US); *Schmalzel 1854* (MO); *Tyson 7099* (NA); *Wilbur, Weaver, Foster, Correa 10879* (CAS, CR, F, MO); *Wilbur & Teeri 13248* (CAS, F).

For any further study, the following materials exist at CIAT as germplasm accessions: *Hernández X-16694*

(G40542); *Freytag & Vakili 78-Guat-18* (G40560); *Debouck & Araya 2091* (G40595); *Debouck, Araya, González & Camacho 3107* (G40762); *Debouck & Soto 1617* (G40798); *Debouck & Soto 1624* (G40785).

DISCUSSION

The afore-mentioned facts about the new taxon elicit the following points for discussion, in relation to its taxonomic identity, taxonomic position, and ecology. **First,** the habit of the plant forming a small colony, structure of the pseudoraceme, size and slow unfolding of the floral parts (the lobation of the calyx is noteworthy), morphology of the pod, and lack of development of one seed, all suggest a relationship with the *Brevilegumeni*, and particularly *P. oligospermus*. This however remains a working hypothesis, pending chromosomal study to discard a relationship with the *Falcati* Freytag (where $2n = 2x = 20$ instead of 22 usually found in the genus: Maréchal 1970; Lackey 1980; Mercado-Ruaro & Delgado-Salinas 1996), and molecular evidence, for instance nuclear ribosomal ITS sequencing (Delgado-Salinas et al. 2006; Serrano-Serrano et al. 2010). On the other hand, although the authors have not had *P. campanulatus* in cultivation for a direct comparison with *P. hygrophilus*, there are enough differences in primary bract, bracteole and flower (Freytag & Debouck 2002, p. 224) to consider that the latter is not a disjunct group of populations of the former, as it happens for *P. tuerckheimii* across its range. *P. tuerckheimii* is indeed scattered in woodlands of high mountains of Chiapas, central Guatemala, central Honduras, eastern Costa Rica and western Panama just as in biogeographic "islands" (Standley & Steyermark 1946; Lackey & D'Arcy 1980; Breedlove 1986; Araya-Villalobos et al. 2001; Debouck 2010b; Zamora 2010). **Second,** *P. hygrophilus* thrives in premontane wet/ rain forests with 1–3 months of dry season (Fig. 5, in/ around biotic unit 1); in that habitat, one usually finds legumes of Desmodieae instead those of Phaseolinae given the challenge for pod opening and seed dispersal. *Phaseolus oligospermus* in contrast is found in subhumid premontane forests with 3–4 months dry season (Araya-Villalobos et al. 2001) (Fig. 5, in/ around biotic unit 4; Fig. 6). *Phaseolus tuerckheimii* and *P. dumosus* Macfady. thrive in humid montane forests at higher altitudes (Freytag & Debouck 2002; Zamora 2010; Fig. 6), where the dry season is longer or well-marked (Fig. 6). From the map (Fig. 5), it seems that a few more areas combining the right altitude, rainfall amount and pattern and other ecological conditions could exist along the Talamanca mountain range, where a large protected area has been established (i.e. 'Parque Internacional La Amistad'), but with grazing on its lower Pacific slopes (Gómez-Pignataro 1986) and in the distant buffer zone (Sánchez-Azofeifa et al. 2003). The total number of populations of *P. hygrophilus* for Costa Rica might be higher than two but possibly not more than a dozen (from a study of the ecological maps: Bolaños & Watson 1993; Herrera-Soto & Gómez-Pignataro 1993), and additional sampling in the Reserva Forestal Los Santos would be a logical starting point. The case of *P. talamancensis* Debouck & Torres calls for caution sure enough in concluding about endemic species: this taxon was initially thought to have its distribution restricted to the Talamanca mountain range in Costa Rica with two populations (Torres-González et al. 2001), and it currently has four known populations, one of them outside that mountain range (Debouck 2010a; Zamora 2010). **Finally,** it is interesting to note that the number of species of *Phaseolus* continues to increase with the disclosure of more endemic species, this time towards the southern part of the range of most species in western Mexico (Delgado-Salinas 1985; Freytag & Debouck 2002; Ramírez-Villegas et al. 2010). For Costa Rica, the number of wild bean taxa has almost doubled since the early floristic work of Paul C. Standley (1937); including the new species here described, ten wild species of *Phaseolus* are now known from there (Zamora 2010).

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BOOK REVIEW

CHARLES D. STUTZENBAKER. 2010. **Aquatic and Wetland Plants of the Western Gulf Coast.** (ISBN 978-1-60344-222-0, pbk.). Texas A&M University Press, John H. Lindsey Bldg., Lewis Street, 4354 TAMU, College Station, Texas 77843-4354, U.S.A. (**Orders:** www.tamupress.com; 800-826-8911). $40.00, 465 pp., 477 b/w photos, map, 236 line drawings, 8½" × 11".

For wetland scientists working along coastal Louisiana and Texas, no other book has been coveted as much as Stutzenbaker's *Aquatic and Wetland Plants of the Western Gulf Coast.* Originally published by the Texas Parks and Wildlife Department in 1999, this A&M edition is not a revision or update, but puts back into print this highly sought after book. While it is not an update, that shouldn't suggest that information is lacking. Rather, it still retains the quality information that has made it such an indispensable book for botanist and landowners of the region.

More than 200 species of wetland plants found from New Orleans, LA, to Brownsville, TX, are collected here along with detailed information for each species and black and white botanical illustrations and photography. Environmental requirements, wildlife values, and propagation and management features are also included for each species. Plant descriptions are arranged by growth characteristics, ranging from free-floating aquatics to trees. Each species gets two pages, a large black and white illustration on one page, juxtaposed by the textual information and some black and white photos on the other page.

This A&M edition does include a "List of Nomenclature Changes" for more than 40 species that were listed in the 1999 edition that are now recognized by recent changes to their classification. This is a welcome inclusion to the text that reinforces its value to those utilizing it for its primary purpose, plant identification. The book begins with an introduction to the western gulf coast, including brief discussions of habitat types, national and regional wetland indications, wildlife values, propagation, and management. This section is followed by the individual plant descriptions, and closes with a glossary, wetland indicator categories, bibliography, and index.

Not to sound unappreciative, but this reviewer will admit that looking at this text with a critical eye has exposed some shortcomings. The books dimensions are 8.5" ×11" and totals more than 400 pages, or approximately one inch of paper. For those considering its use in a backpack for fieldwork, you should know it will take up a lot of space and it is heavy. Having it in your vehicle when you return with a bag full of voucher specimens, on the other hand, is a reasonable compromise. While the black and white botanical illustrations are useful and well annotated with key identification characteristics, the black and white photography is not extremely helpful. Considering my comment about size, this seems like the first place one could go to condense the book. Color photos of the plant species would better justify the inclusion of some photos and size of the book.

Ultimately, this is the exact same book as the 1999 edition, but with a more eye-pleasing cover. Considering the incredible demand for the book, it is regrettable that a more extensive update was not considered. This reviewer once observed a price of US $500.00 for a used copy through an online retail store. Doubtless, this demand will be quenched with the publication reviewed here. But, it also reminds us that a wetlands field identification book with color photography and pocket-size is still absent in a market with obvious demand. Overall, I recommend this book to wetland scientists and laypersons working in the Gulf Coast.—*Kevin Janni, Botanist, SWCA Environmental Consultants and BRIT Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

LEPECHINIA YECORANA (LAMIACEAE), A NEW DIOECIOUS SPECIES FROM THE YÉCORA AREA OF SONORA, MEXICO

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ABSTRACT

Lepechinia yecorana is described as new from an area of volcanic ash soil in the Yécora area of Sonora, Mexico. The species is most closely related to *Lepechinia mexicana*, but differs from the latter in its narrower, less strongly vestitured leaves, its smaller white, purple-spotted corollas with a distinctive vestiture pattern within, and its more abundant flowers either solitary or in 3-flowered axillary cymes. Both taxa are functionally dioecious, a feature otherwise known only in *Lepechinia* in the South American section Parviflorae.

RESUMEN

Se describe como nueva para la ciencia **Lepechinia yecorana,** procedente de un área con suelos de cenizas volcánicas en la zona de Yécora, Sonora, México. La especie está estrechamente relacionada con *Lepechinia mexicana*, pero difiere de ésta última por sus hojas más angostas y menos tomentosas, sus corolas más pequeñas, blancas con manchas púrpuras, con un patrón de indumento distintivo en su parte interna y por sus flores más abundantes dispuestas ya sea solas o en cimas axilares 3-floras. Ambas especies son funcionalmente dioicas, característica conocida para *Lepechinia* sólo en la sección Parviflorae de América del Sur.

INTRODUCTION

The broad Río Mayo floral region covers most of southern Sonora from the Sinaloan border to the Río Yaqui in the north (Martin et al. 1998). The completion of Mexico Federal Highway 16 (MEX 16) in 1992 provided improved access to this portion of the Sierra Madre Occidental in easternmost Sonora (Búrquez et al. 1992; Van Devender et al. 2005). The flora of the Municipio de Yécora, in the northern portion of the Río Mayo region, is very diverse with over 1770 taxa in 3,300 km². Floristic publications in the area include the flora of the unique sphagnum spring at the Ciénega de Camilo east of Maycoba, 10 km east of the Chihuahua border on MEX 16 (Van Devender et al. 2003) and a summary of the distribution of the grasses in the Municipio (Van Devender et al. 2005). The Yécora area has steadily yielded a wealth of range extensions and new species in the last two decades.

We describe herein a species of Lamiaceae that is restricted to pinyon-juniper-oak woodland on mottled pink and whitish volcanic ash in the Yécora area. In its small shrub habit and solitary flowers, the taxon appears most similar to *Lepechinia mexicana* (S. Shauer) Epling [= *Sphacele mexicana* S. Shauer], a shrub species occurring in Nuevo León, Tamaulipas, Veracruz, San Luis Potosí, Jalisco, Hidalgo, Querétaro, Puebla, and Oaxaca. Both are well-branched shrubs with small, bullate upper leaf surfaces, with forked to dendritic vestiture, and with solitary, axillary flowers. However, *L. mexicana* occurs in rather arid habitats and has thickened, strongly vestitured leaves and moderately large blue-lavender corollas mostly (8–)9–12 mm long, while the new species occurs at higher elevations among pinyons and yellow pine and, at least at the type locality, the leaves are narrower, thinner, more flaccid, less conspicuously bullate, and the corollas are white with purple spots at the throat and on the abaxial limb and only 5–7 mm in length. The less rigid leaves could be explained away as the plants occur in a more mesic habitat. Further observations found that both *L. mexicana* and the new taxon appear to be functionally dioecious—a feature otherwise known only in South American species of *Lepechinia* section Parviflorae Epling. But first a look at the genus as a whole.

Bentham recognized both *Lepechinia* Willd. and *Sphacele* Benth. in de Candolle's Prodromus (Bentham 1848) and Genera Plantarum (Bentham 1876) in each case within his tribe Satureineae (ovary 4 parted, nutlets dry, the areole oblique, small); subtribe Lepechinieae, (calyx loosely campanulate to broadly tubular, irregularly veined, corolla tube ± broad, lobes ± bilabiate, flat), which included the genera *Lepechinia*, *Sphacele*, *Dekinia,* and *Horminum*. Bentham (1876) distinguished *Lepechinia* (with 2 species) as tending to have inflexed calyx teeth, non-annulate corolla tubes (i.e., lacking a pilose ring of hairs within), oblong, and parallel anther lobes vs. *Sphacele* (with 20 species) with more open calyces, the corolla tubes with a ring of hairs in the tube (an annulus), and linear, divergent to divaricate anther locules. Epling (1948) submerged *Sphacele* within *Lepechinia*, and noted that the monotypic *Dekinia* is synonymous with, and correctly placed in, *Agastache mexicana. Horminum* is still recognized as a genus of high-elevation European species.

Epling's *Lepechinia* is a diverse genus of about 36 species (Hart 1983), consisting of perennial herbs, shrubs, small trees with often large, petiolate, narrowly to broadly ovate to deltate-hastate leaves with veins often strongly impressed above (the surface bullate) and raised beneath and with hairs often branched. Flowers may be large or small, borne in inflorescences ranging from lax, open or glomerate, cymose verticils arranged in panicles to dense spikes or with inflorescences reduced to single flowers in the axils of the upper leaves or bracts. Calyces are 5 toothed, 5–10 veined, variously 2 lipped, accrescent and loosely surrounding the developing nutlets with the cross veins sometimes thickened forming a reticulate pattern on the persisting calyces. Corollas are bilabiate, with the broad tube shortly exserted from the calyx, the lobes ± plain (flat), the abaxial one largest, the stamens are 4, short exserted to included. The nutlets are ovoid, black, stony, smooth (rarely reticulate), glabrous (rarely puberulent), and the basal hilum is small, and asymmetrical. Most species have hermaphroditic flowers, but some species from South America are gynodioecious, or dioecious.

Epling (1948) recognized eight sections within his *Lepechinia*, and the above noted *L. mexicana* fell into his section Calycinae, with the strongest shared characteristic being the presence of solitary axillary flowers. The other species in the section are rather distinctive species from southern California and adjacent Baja California, Mexico, forming a homogeneous group quite different from *L. mexicana*. The California species are more suffrutescent than shrubby, have large hastate-cordate leaves, large, open flowers, solitary in the leaf or bract axils on sometimes long peduncles/pedicels. The calyces are broadly campanulate, ± membranous, with acicular teeth, and they greatly expand and become strongly veined after flowering. *Lepechinia mexicana* occurs in drier habitats in central Mexico, is a shrub, with much smaller leaves and corollas with a protruding lower limb and shorter style lobes. The only feature in common with the other species in section Calycinae is the presence of solitary, axillary flowers. It appears doubtful that the relationships of *L. mexicana* lie with section Calycinae. The herbaceous Peruvian *L. tomentosa* (Benth.) Epling, of section Lepechinia Epling also has solitary, axillary flowers. Epling (1948) noted that *L. mexicana* showed relationships with *L. tomentosa* of Peru and with the South American members of section Speciosae Epling.

Hart (1983) in his unpublished dissertation retained *Sphacele* in what he considered a polyphyletic *Lepechinia*, placing all but one of Epling's sections, including the type species of *Sphacele,* in his section Lepechinia (from California to Argentina, with 24 species) and retained section Parviflorae for 12 South American dioecious-gynodioecious species. Plants of section Parviflorae are shrubs to small trees, the leaves are large, broadly to narrowly ovate, cordate to cuneate above a slender to decurrently winged petiole, the blades are variously bullate, crenate-serrate, glabrous or vestitured. The flowers are produced in often well branched verticillate, spicate, or paniculate inflorescences and the flowers are uniformly small, with corollas 2–5(–8) mm long, white, with purple markings on the largest abaxial lobe, (as in the new taxon here described). They have a pubescent patch on the inner distal corolla throat between the two abaxial stamens and lack a ring of hairs in the lower tube (the annulus). The staminate flowers are similar in color to the pistillate flowers, but slightly larger, have four fertile stamens, and a usually non-functioning style. The pistillate flowers have four much-reduced sterile stamens and a functional ovary.

Hart's (1983) section Lepechinia (that contained the rest of the genus) is quite variable and admittedly

polyphyletic (p. 156), including both herbs and shrubs, with large or small leaves, and variously branched inflorescences (as above), or the flowers solitary in the leaves-bracts, and the flowers larger, and hermaphroditic (gynodioecious in 2 species, one from Haiti the other from Columbia-Venezuela). Corollas range from 5–40 mm in length, and range from blue, purple, red, yellow or white in color, and they have a ring of hairs that form an annulus in the lower tube, though this is sometimes poorly developed. They range from central Mexico to Argentina. Hart (1985) in his publication on dioecy in *Lepechinia*, used Epling's sectional classification, placing the gynodioecious species outside the section Parviflorae in section Salviifoliae Epling.

It appears, however, that both *L. mexicana* and the new taxon are dioecious. In the new taxon, from which one of us (JH) has made mass population collections, both staminate and pistillate flowers have a fully formed ovary-style-stigma, (the pistillate flowers have a fertile ovary, but four reduced staminoda, the staminate flowers have 4 fertile stamens and a sterile ovary (Fig. 1 A-B). Only one developing fruit was found in staminate plant specimens, which would make that plant polygamodioecious. All pistillate plants, of course, produced fruit. The corollas in the new taxon are white, small, slightly larger in staminate than pistillate flowers (as in the South American section Parviflorae) (see Fig 2) and both staminate and pistillate flowers have a well defined annulus in the lower tube [as in Hart's (1983) section Lepechinia] but the hairs are continuous along the corolla tube-throat floor to the area between the abaxial filaments unlike either section (see Fig. 1 A-B). In contrast, flowers in section Parviflorae have an internal patch of hairs only between the abaxial filaments and an annulus is absent. The reproductive condition in *L. mexicana* is less resolved. Few flowers or fruit were found in the specimens examined. Staminate flowers were observed, as were flowers with aborted anthers, and as in the new taxon, both staminate and pistillate flowers had fully formed styles. But as the specimens had few flowers, it was not possible to make many observations.

The new taxon and *L. mexicana* appear to represent an independent origin of dioecy in the genus. It is interesting that, at least in the new taxon, it has conformed to certain features also found in section Parviflorae (i.e., small white corollas that are slightly larger in staminate flowers, the retention of staminoda in pistillate flowers and of a style in staminate flowers). But whereas in section Parviflorae the white corollas have purple spots on the largest abaxial lobe, in the new taxon there are purple spots along the rim of the throat, with a few on the abaxial lobe. Furthermore, the new taxon has a basal annulus, hairs between the abaxial filaments, and a continuous patch of hairs between the abaxial filaments and annulus (Fig.1, A–B).

SYSTEMATICS

Lepechinia yecorana Henrickson, Fishbein, & T. Van Devender, sp. nov. (**Figs. 1A–E, 2**). Type: MEXICO. Sonora: Mpio. de Yécora, 1.6 km W of Chihuahua border, 15.5 km E of el Kipor on MEX 16, pinyon-juniper-oak woodland on white volcanic ash slope, flowers white, leaves aromatic with light anise odor; near 28°26'09"N, 108°31'22"W, 1600 m, 29 Mar 1997, *T.R. Van Devender 97-854, with A.L. Reina-G., G.M. Ferguson, D. Larson, M.J. Martínez, and C.P. Martin* (holotype: ARIZ, isotypes: MEXU, TEX, USON, and to be distributed).

Vestimento brevi, sparso, pilo dendritico, cum brachio radiali soli 0.1 mm longitudine; foliis tenuibus, angustibus, lanceolatis, saepe basaliter dentatibus, plerumque 3.3plo longioribus quam latioribus; calyce subanthesi cum lobis curtis; corolla alba cum punctis purpuris, 5–6.5 mm longa; floribus solitariis vel in cymae cum tribus floribus in axillis foliorum dispositae; ab *Lepechinia mexicana*, species similaris, autem vestimento alba tomentosa, cum brachio radiali usque ad 0.3 mm longitudine, foliis crassioribus, oblongis-ovatis, plerumque 1.5plo longioribus quam latioribus; calycis lobis tubum fere aequantibus; corolla caesia vel violacea, 8–15 mm longa; cum floribus semper singularibus in axillis foliorum, differt.

Rounded to spreading, oppositely, usually densely branched, suffrutescent, dioecious (rarely polygamodioecious) shrubs to 1.2 m tall. Young stems slender, erect to spreading; internodes 3–15(–24) mm long, initially 4 ribbed, soon rounded, often ± purplish-red, pubescent with ± thick-based, translucent, simple to distally forked or alternately branched dendritic hairs 0.02–0.2(–0.4) mm long, the lateral hair branches thick to slender, to 0.05–0.1(–0.15) mm long, also with scattered clear, sessile glands to 0.08 mm in diameter. Leaves opposite, decussate, lanceolate, ± hastate, 13–20(–26) mm long, (2.6–)4–6(–9) mm wide, [leaf length/width ratio 1.9–3(–4)] bluntly acute to obtuse at the tip, with a single pair of short, divergent teeth in the lower third (or these absent in some leaves), truncate to abruptly cuneate below to a typically broadly tapered, winged

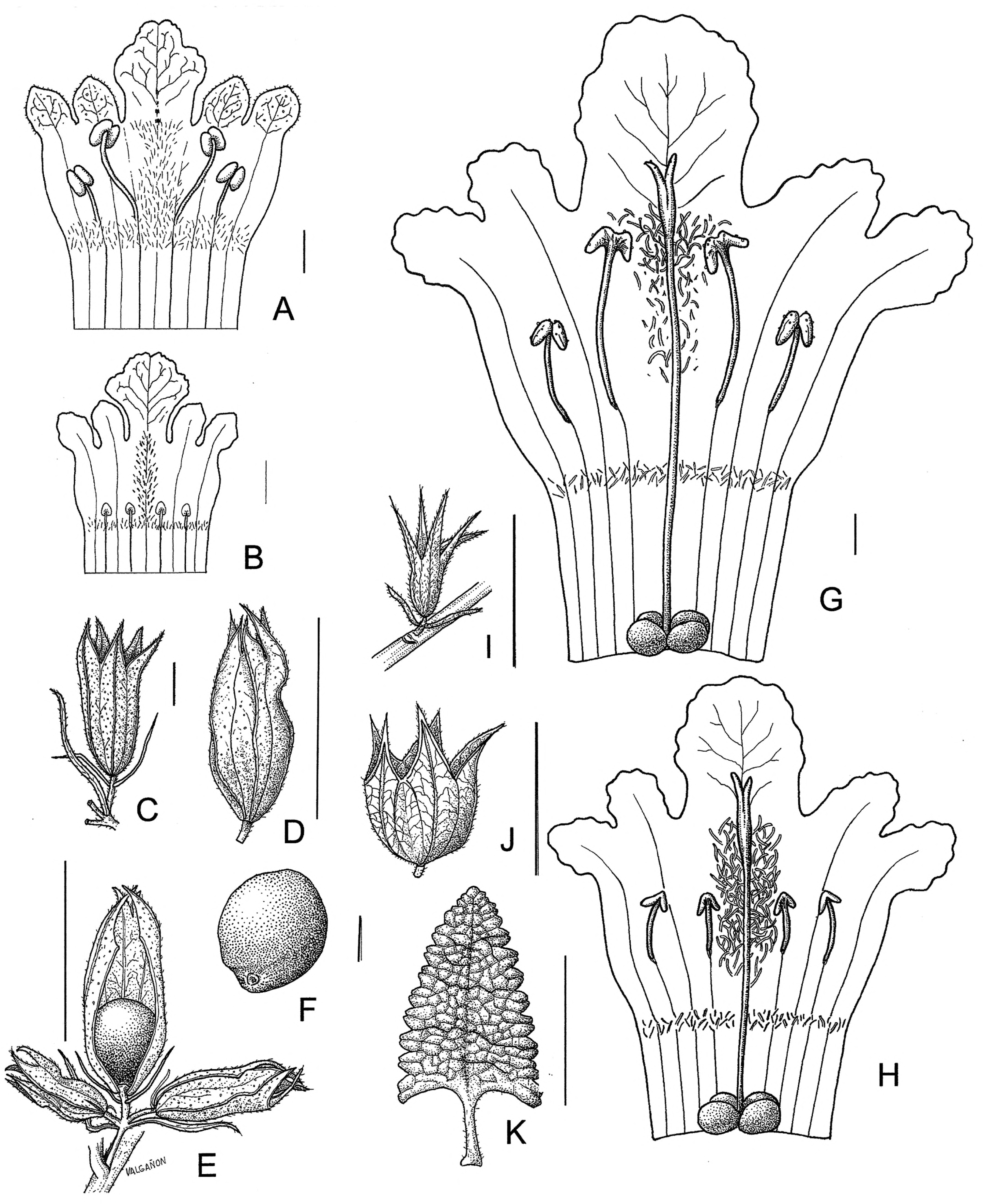

Fig. 1. Comparison of *Lepechinia yecorana* and *L. mexicana*. **A–E.** *Lepechinia yecorana*. **A.** Staminate corolla expanded, cut between the adaxial lobes, note large abaxial corolla lobe, subequal lateral and adaxial lobes, pubescent annulus and continuation of hairs onto the abaxial throat, longer abaxial, shorter adaxial filaments and larger, fertile anthers. **B.** Pistillate corolla expanded, showing smaller size, note reduced staminodes with short filaments, smaller anthers. **C.** Calyx at anthesis showing bract and bractlets. **D.** Fruiting calyx, note poorly developed horizontal venation. **E.** Triad of post-flower calyces, the upper cut open showing nutlet. **F.** Nutlets are hard, black smooth with a asymmetrical attachment scar. All from liquid-preserved material of Henrickson 24629. **G–K.** *Lepechinia mexicana*. **G.** Staminate corolla expanded (as in A) showing annulus, local patch of larger hairs in throat, fertile stamens, and showing ovaries, style and style lobes that do not mature. **H.** Pistillate corolla expanded (as in B) showing smaller size, note reduced staminodia, annulus, and patch of long hairs on corolla throat and fertile gynoecium. **I.** Calyx at anthesis showing bractlets, longer sepal lobes. **J.** Fruiting calyx, often with 2–3 nutlets are broader and have stronger development of lateral venation. **K.** Mature leaves are thicker, more strongly bullate, more ovate. G–J from *Cisneros 2417* (TEX-from Puebla); H, I, K from *Chiang et al. 2413* (TEX-from Oaxaca). Scale: short bars = 1 mm; long bars = 1 cm.

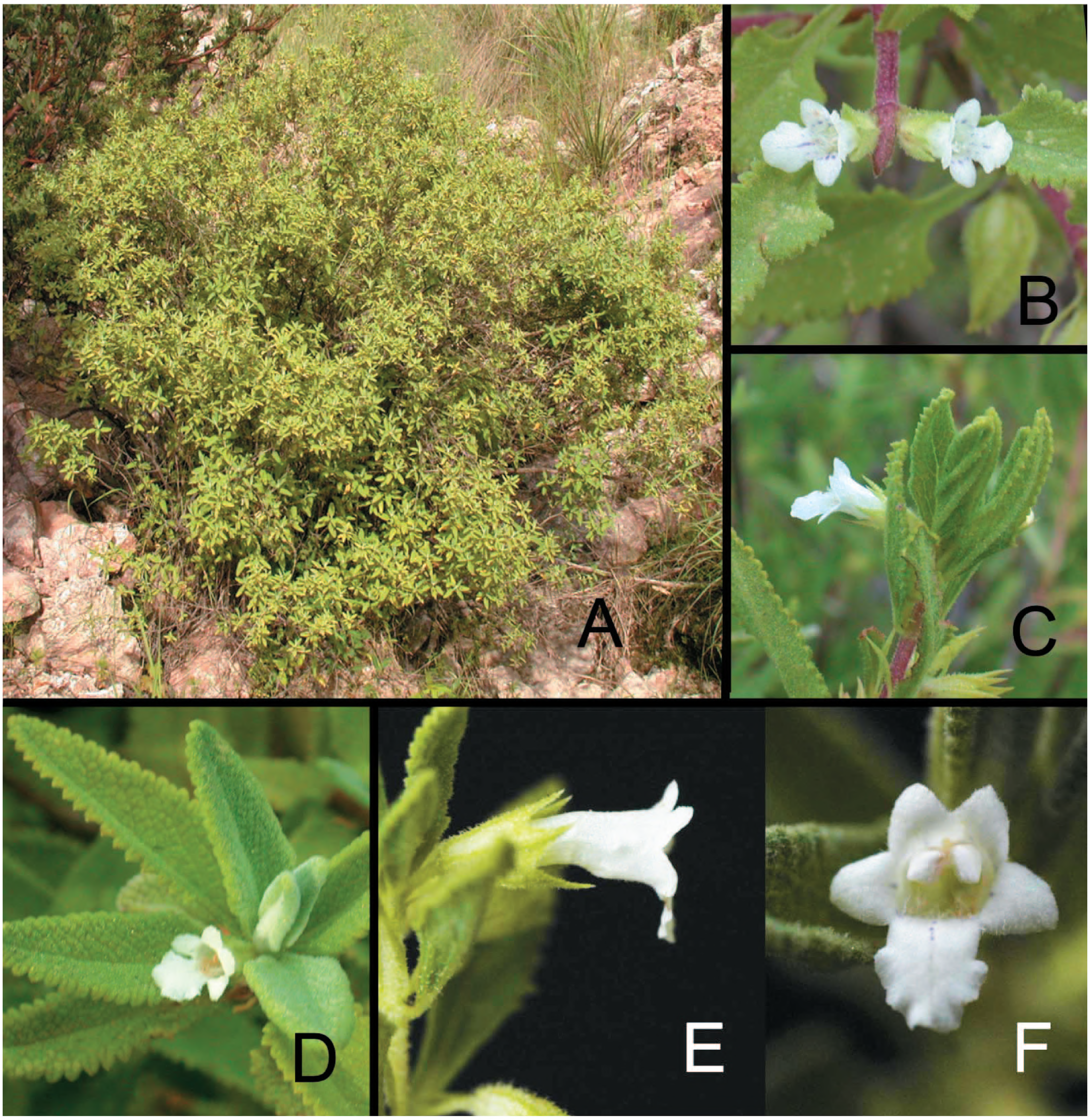

Fig. 2. ***Lepechinia yecorana*****. A.** **Plant habit. B–C. Pistillate flowers, top-face view showing lavender spots on corolla, red stems in B, young leaves in C. D. Staminate flower, face view showing white anthers in upper corolla throat. E. Pistillate flower side view showing a drooping abaxial corolla lobe. F. Leaf and developing calyx. G. Partially mature calyces revealing single nutlets within, note lack of horizontal vein thickening. H. Same, cut open to show single nutlet. All from** ***Henrickson 24629*****.**

petiole 3.6–7(–10) mm long (but cordate when the lateral teeth are closer to the base), the margins straight to ± concave, uniformly and closely toothed, but the teeth margins revolute and the margins appearing crenulate, the crenulations 11–14 per 10 mm of margin, the upper surface bullate-rugose with weak to strongly impressed veins, the veins distinctly raised beneath, the blades ± thin, (more thickened and then coarsely bullate with increased aridity) closely pubescent with simple, forked to alternately branched hairs (0.02–)0.1–0.35 mm long and with yellowish glands to 0.08 mm wide on both surfaces but often more dense abaxially, the developing and youngest leaves gray canescent with a closer vestiture. Flowers spreading to ascending, usually solitary in each leaf axil, (2 per node, 1 per leaf axil) or in robust plants in axillary 3-flowered dichasia; basal peduncles 0.5–1.5 mm long; paired bracteoles linear-oblanceolate to subulate, 2–7 mm long, 0.2–0.4(–0.5)

mm wide, green, entire with a strong midvein; pedicels 0.5–1(–2.0) mm long, when flowers 3 per axil, the lateral flowers developing in bractlet axils on peduncles, with paired narrow bracteoles and pedicels; the peduncle/pedicels and bracts all vestitured as the leaves. Calyces narrowly ampliate, 2.8–3.7 mm long in pistillate flowers, 3.5–4 mm long in staminate flowers, the 5, narrow, attenuate lobes (1.0–)1.5–2 mm long, subequal, their margins straight to concave, tapering to a muticous tip, the basal sinuses acute, each with a prominent, straight vein to the lobe tip, the lateral venation irregularly reticulate, the calyces vestitured ± as the leaves, in pistillate flowers becoming ± inflated around the developing nutlet(-s), 7–9.5 mm long, 3–5 mm wide, reticulately veined above with the vertical veins ± thickening, the horizontal venation not much thickened, their calyx lobes distally converging and overlapping. Corollas bilabiate, white, with purple dots around the distal tube and in a medial line down the largest (abaxial) lobe, 4.7–5.2 mm long in pistillate flowers, 5.7–6.5 mm long in staminate flowers (wetted), the basal tube cylindrical, 1.3–1.5 mm in diameter, 1.2–2 mm long, hirtellous outside with simple or branched hairs, with an internal annulus of crinkled hairs 0.3–0.4 mm wide, 1.1–2.2 mm above the base inside, the hairs 0.3–0.5 mm long, continuing onto the abaxial throat to between the abaxial anthers; corolla throat slightly compressed 1.5–2.1 mm long, 1.1–1.7 mm tall, 1.5–2.2 mm wide, the outside marked with angled protrusions at the filament bases in staminate flowers, closely hirtellous with branched hairs outside; corolla lobes 5, the abaxial lobe largest, ± flattened, extending forward (porrect) or descending, obovate, obtuse-rounded, 1.7–2.7 mm long, 1.9–3.0 mm wide, marginally crenate, narrowed to a broad basal neck 1.2–1.9 mm wide, the lateral two lobes ovate, ± obtuse, ±0.9–1.3 mm long and wide, ± concavo-convex, spreading, the adaxial two lobes, obliquely ovate, 0.7–1.2 mm long, 0.9–1.4 mm wide, erect, slightly reflexed. Stamens 4, in staminate flowers the abaxial pair with filaments 1.0–2.0 mm long, upcurved distally, the anthers ovate, exserted, 0.6–0.7 mm long, 0.5 mm wide, the thecae slightly divergent, the adaxial stamens with filaments 0.6–1.0 mm long, their anthers similar, included, situated behind the anthers of the abaxial pair on the distal upper throat, the staminate flowers also having normal appearing ovaries and a white style 3.3.7 mm long, but the stigma apparently not opening; in pistillate flowers the staminodes produced just distal to the annulus, uniform in size, the filaments poorly developed, to 0.2 mm long, the anther sacs 0.25–0.4 mm long, sterile. Ovaries 4, in pistillate flowers subglobose, each 0.25–0.35 mm in diameter, white, smooth (borne on a basal discoid gynophores) 0.6–1 mm wide, 0.3–0.4 mm tall; style extending from between the ovaries, 3.2–4.3 mm long, glabrous, white, exserted beyond the anthers, the lanceolate style lobes 1.5–0.3 mm long, the abaxial lobe longer. Fruit a schizocarp of usually only 1(–2), ± globose, dull brown-black, smooth mericarps (nutlets), these glabrous, 2.5–3.0 mm long, 2.0–2.5 mm wide, often compressed and to 2.0 mm thick, the wall 0.22 mm thick, hard, the attachment point offset from the base, slightly depressed, ± 02 mm long.

Additional collections: **MEXICO. Sonora:** Mpio. de Yécora, 1.6 km W of Chihuahua border, 15.5 km E of el Kipor on MEX. 16, pinyon-juniper-oak woodland on white volcanic ash slope, dominant shrub, half the plants with fruit, some with both old and green fruit, 28°26’09”N, 108°31'22"W, 1600 m, 25 Sep 1997, *Reina-G. 97-1428 with Van Devender* (ARIZ, TEX and to be distributed); same area, 29 Mar 1996, *Van Devender 97-394 & Reina-G.* (TEX); same area, 14 Aug 2003, *VanDevender et al., 2003-897* (ARIZ); same area, 10 Aug 2009, *Henrickson 24692* (ARIZ,TEX and to be distributed); along Hwy 16, 7.9 km E of el Kipor, ca. 1 km W of Chihuahua state line, pinyon-juniper-oak woodland, 28°26'N, 108°31.5'W, 1600 m, 15 Aug 1998, *Fishbein et al. 3614* (WS); 2.1 km W of Arroyo Hondo, 6.1 km W of Chihuahua border on MEX 16, open pinyon-juniper-oak woodland on steep pink and white mottled volcanic ash slope, 28°26'24"N 108°33'20"W, 1400 m, 25 Sep 1997, *Reina-G. 97-1364 & Van Devender* (ARIZ).

DISCUSSION

In its small shrub habit, axillary flowers, and small leaves, *Lepechinia yecorana* appears most similar to *Lepechina mexicana*. Leaves of *L. mexicana* tend to be broader, truncate to cordate above narrowly winged petioles and invariably are thicker, more rigid, and with thickened, raised veins on the abaxial surface. In most collections of *L. yecorana* the leaves are much thinner, weakly bullate, and weakly vestitured, but not in *Van Devender 97-394*, which has much strongly vestitured, thickened leaves with cordate bases—apparently collected during a more arid season. It appears that leaf texture features are influenced by environmental factors.

Flowers of the two species are of similar configuration (Fig. 1), but the corollas of *L. mexicana* are larger (9–15 mm total length), lavender, purplish, or blue, with small white spots, the filaments are longer, the divergent anther sacs are longer (0.8–0.9 mm) and the calyx lobes are longer and more attenuate, (2.5–4 mm long, to 5.6 mm long in fruit), the calyces become widely inflated in fruit around a larger number of nutlets, and the cross veins typically thicken as is characteristic of *Lepechinia*. In addition the hairs of the annulus are not continuous with the hairs at the base of the central lobe in *L. mexicana*, as they are in *L. yecorana*. However, it must be mentioned that a specimen from near the city of San Luis Potosí, some 1000 km to the south-southeast, also has smaller, white, purple-spotted flowers (± 6.9 mm long) but the specimen has broader, ovate, thickened leaves as in *L. mexicana*.

Hart (1983, 1985) noted that dioecy is rare in the Lamiaceae, previously known only in the South African genus *Iboza* N.E. Br. (Brown et al. 1910), which has been transferred into *Tetradenia* Benth. (Codd 1983), and in section Parviflorae of *Lepechinia*. In *Lepechinia* Hart noted that dioecy evolved from gynodioecism at least two times in section Parviflorae. The situation in *Lepechinia yecorana* and *L. mexicana* appears to be an independent origin of dioecy in the family. In these, flowers of both sexes have styles, but in the male flowers the styles are not functional, except in rare instances where male plants produce fruit, making the species rarely polygamodioecious. It is remarkable that the flowers of *L. yecorana* are similar in size and coloration to those of *Lepechinia* section Parviflorae. Ana L. Reina-G. was the first to note that the new taxon exhibited dioecy "about half of plants with fruit" (*A.L. Reina-G. 97-1428*- in herbarium).

Other species of *Lepechinia* present in pine-oak forests in the Río Mayo region in Sonora include *L. caulescens* (Ortega) Epling in Sierra Saguaribo at 1430 m (Martin et al. 1998) and on Mesa del Campanero at 1740–2150 m (ca. 69 km W of the westernmost *L. yecorana* locality, Martin et al. 1998). Also *L. schiedeana* (Schltdl.) Vatke occurs at 1700–2200 m in pine-oak forest near the cascada de Basaseachic, Chihuahua (about 60 km E on MEX 16 of the eastern *L. yecorana* locality; Spellenberg et al. 1996; Martin et al. 1998). Both of these species have much larger leaves: *L. caulescens* is a white-flowered, colonial herb with flowers in dense, elongated terminal heads; *L. schiedeana* is a blue-flowered, rhizomatous herb with flowers in terminal verticils.

In the Municipio de Yécora, pine-oak forest occurs from 1200–1700 m elevation with oak woodlands on drier exposures at 1,000–1275 m (Van Devender et al. 2005). The Sierra Madre Occidental in this area is formed of rhyolites and andesites of Oligocene and Miocene ages (Cochemé & Dement 1991). Unusual volcanic substrates support distinctive local plant distributions and associations in many areas in the Municipio de Yécora. Areas with hydrothermically-altered, acidic volcanic soils termed glossans typically support pines and oaks at low elevations in the tropical deciduous forest zone (Goldberg 1982). The *Lepechinia* sites at 1400 and 1600 m elevation present the opposite situation with relatively xeric pinyon-juniper-oak woodland in local areas with white or white and pink mottled volcanic ashes surrounded by more mesic pine-oak forest.

Vegetation at the *Lepechinia* localities is a locally unique pinyon-juniper-oak woodland unlikely to be found elsewhere. Dominants include *Pinus discolor* D.K. Bailey & Hawksw. and *Juniperus durangensis* Martínez with occasional *Quercus oblongifolia* Torr., *Q. toumeyi* Sarg., and *Q. viminea* Trel. Shrubs include *Arctostaphylos pungens* H.B.K., *Erythrina flabelliformis* Kearney, and *Garrya wrightii* Torr., while *Mortonia* sp., *Aralia humilis* Cav., *Berberis pimana* Laferr. & Marroq., and *Comarostaphylis polifolia* (H.B.K.) Zucc. were also present at the eastern *Lepechinia* locality.

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COLUMNEA BIVALVIS (GESNERIACEAE), A NEW SPECIES FROM THE EASTERN SLOPES OF THE ECUADORIAN ANDES

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ABSTRACT

Recent field expeditions to the eastern slopes of the Ecuadorian Andes and revisionary work on *Columnea* (Gesneriaceae) section *Collandra* have resulted in the discovery of a new plant species. The new species, **Columnea bivalvis,** is distinguished by the presence of two pendent clasping bracts that enclose a single axillary flower.

RESUMEN

Expediciones recientes a las estribaciones orientales de los Andes Ecuatorianos, y el trabajo de revisión de la sección *Collandra* del género *Columnea* (Gesneriaceae) permitieron el descubrimiento de una nueva especie de planta. La nueva especie, **Columnea bivalvis,** se distingue por tener dos brácteas colgantes que se tocan por sus márgenes encerrando una única flor axilar.

Key Words: *Collandra, Columnea*, Gesneriaceae, Ecuador, Taxonomy, Flora of Ecuador

INTRODUCTION

The genus *Columnea* belongs to the New World subfamily Gesnerioideae. It is the most diverse genus in the subfamily with over 200 species (Skog & Boggan 2006; Weber 2004; Burtt &Wiehler 1995). The subdivision of *Columnea* sensu lato into sections or into segregate genera has caused much controversy and taxonomic confusion (Kvist & Skog 1993; Wiehler 1973, 1983). We recognize the classification based on recent phylogenetic hypotheses that strongly support the monophyly of *Columnea* (Smith 1994; Smith & Sytsma 1994; Clark et al. 2006) and non-monophyly for segregate genera. Thus, the sectional classification outlined in Kvist and Skog (1993) is more desirable as an informal classification until segregate clades can be evaluated phylogenetically.

The new species described here belongs to *Collandra*, the most diverse section in *Columnea*. The following characters are useful for recognizing the species within this section: dorsiventral shoots with anisophyllous subsessile leaves and ovoid (non-globose) berries. In this paper we describe a new species of *Columnea* that is known from two populations between 1800 and 2350 m from the eastern slopes of the Ecuadorian Andes.

TAXONOMIC TREATMENT

Columnea bivalvis J.L. Clark & M. Amaya, sp. nov. (**Figs. 1 & 2**). Type: ECUADOR. Tungurahua. Cantón Baños: parroquia Río Verde, sector Machay, forested trail (from Baños-Puyo road) towards Cascada de San Miguel via San Augustin, 1°23'5" S, 78°16'50"W, 1800–2200 m, 23 Dec 2000, *J.L. Clark, E. Narvaez & J. Vargas 5693* (holotype: US; isotypes: COL, MO, NY, QCA, QCNE, SEL).

Differt a ceteris *Columneis* praesentia unius floris axillaris inclusi in binis bracteis amplectentibus by the presence of a single axillary flower enclosed by a pair of pendent clasping bracts.

Epiphytic vine, suffrutescent, often branched; stem terete, 0.3–0.8 cm, reddish villous (trichomes 7–10 celled), internodes 1–4 cm long. **Leaves** opposite, strongly anisophyllous in a pair, chartaceous; larger leaf with petioles 0.3–0.9 cm long, densely reddish villous; blade asymmetrical, narrow oblong to oblanceolate, 9.5–20 × 2.2–4.2 cm, base oblique, apex acuminate, margin dentate; adaxially green, golden villous (trichomes 5–7 celled) and with sparsely distributed white unicellular setulose hairs, veins not prominent; abaxially

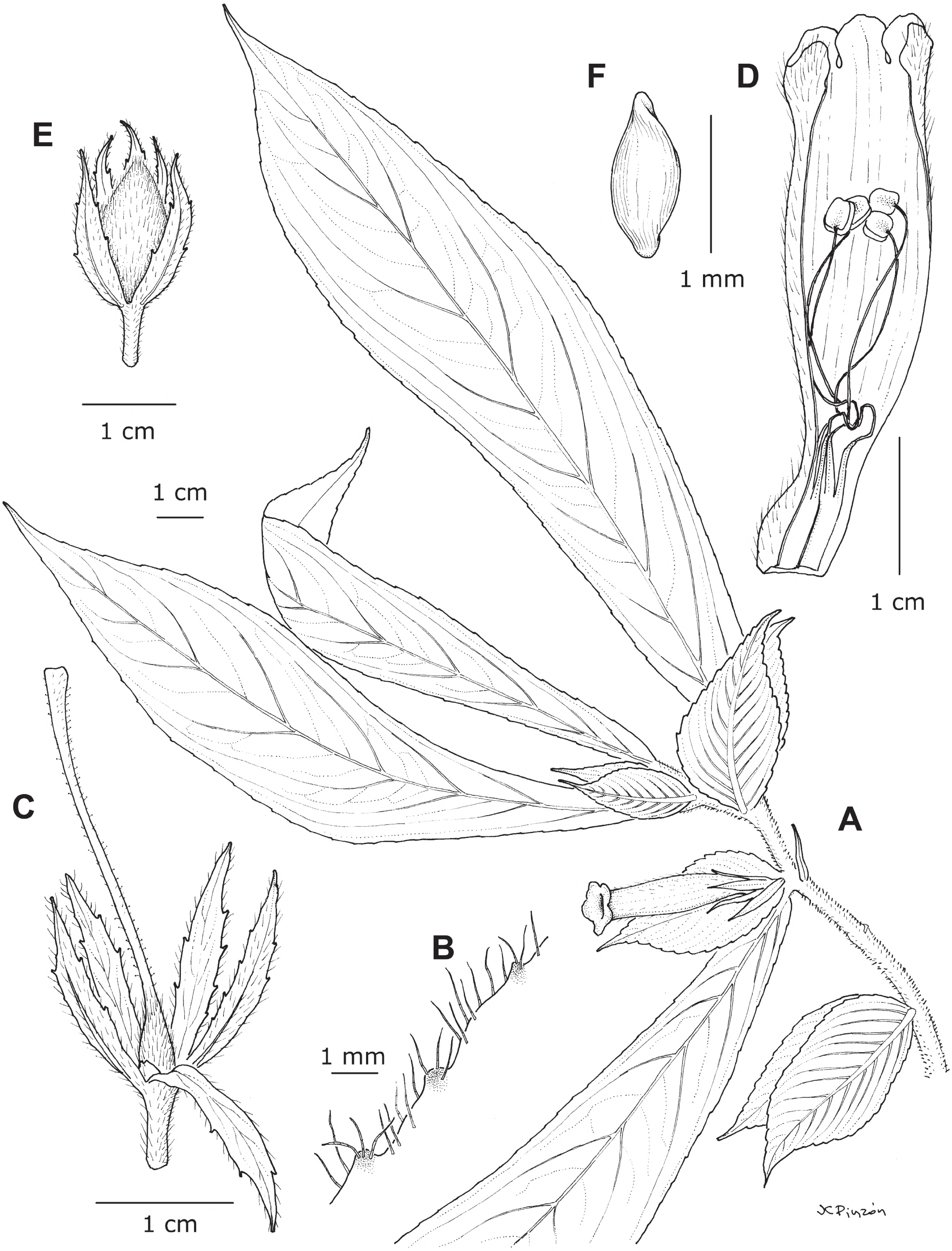

Fig. 1. ***Columnea bivalvis*. A.** Habit and inflorescence. **B.** Enlargment of larger leaf margin. **C.** Calyx and gynoecium. **D.** Corolla and androecium. **E.** Fruit. **F.** Seed.

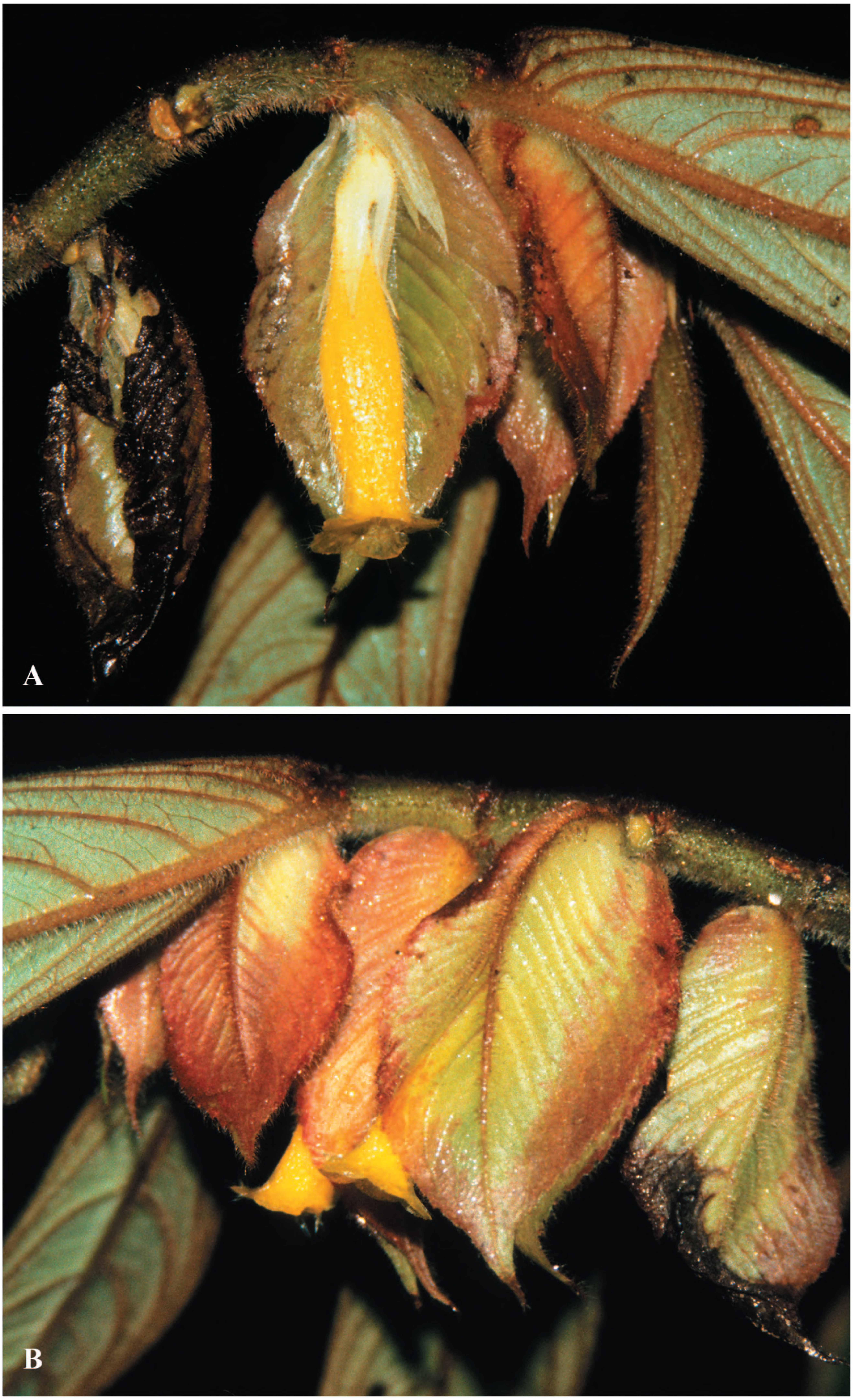

Fig. 2. *Columnea bivalvis*. **A.** One of the paired bracts removed to show uniformly yellow tubular corolla. **B.** Dorsiventral shoot showing pendent bracts (photos by J.L. Clark; from the live plant from which the holotype was collected, *J.L. Clark, E. Narvaez & J. Vargas 5693*).

green with red venation, villous (trichomes 5–7 celled), 8–10 pairs of lateral veins; smaller leaf sessile, blade asymmetrical, oblong, 1.5–2 × 0.3–0.5 cm, base oblique, apex attenuate, margin dentate, adaxially green, reddish villous (trichomes 7 celled), abaxially green, reddish villous (trichomes 7 celled). **Inflorescence** epedunculate with 1 flower per node, larger bracts persistent and paired, green with red margins, outer surface reddish villous, asymmetrical, broadly ovate, 4–4.7 × 2.5–3 cm, bracteoles 2–4, unequal in size, narrowly ovate to lanceolate, 1.2–2.5 × 0.2–1 cm, pedicel 0.2–0.4 cm long, densely villous (trichomes 4–5 celled). **Calyx** pale green; lobes 5, nearly free joined only at the base by 1 mm of their length; narrow oblong, 1.5 × 0.3 cm, margin dentate with three glandular teeth on each side, outside densely villous (trichomes 5–7 celled), inside glabrous. **Corolla** uniformly yellow, tubular, 3.7–4.5 × 0.8–1 cm, basally gibbous and slightly oblique in the calyx, gibbosity 0.4 × 0.5 cm constricted apically 0.3 cm, 0.8–1 cm at the widest part of the tube and constricted again at the limb to 0.7 cm; limb nearly actinomorphic, slightly ampliate in mid region, lobes rounded, subequal 0.3 × 0.3 cm, outside apically sericeous, glabrescent toward the base (trichomes 8–12 celled), inside glabrous. **Androecium** of 4 stamens, filaments 3.2 cm long, glabrous, basally connate for 0.5 cm; anthers oblong 2.0 × 1.3 mm, connective rectangular, 1.8 × 1.2 mm. **Nectary** a single dorsal trilobed gland. **Gynoecium** with the ovary ovoid, 0.7 × 0.3 cm, densely sericeous; style 2.5–3 cm long, laminar with glandular trichomes; stigma bilobed. **Fruit** an ovoid berry, 1.5 × 0.8 cm. **Seeds** light brown 1.8 × 0.5 mm, elliptic, and longitudinally striate.

Distribution and habitat.—*Columnea bivalvis* is only known from two localities in the wet Andean cloud forests in eastern Ecuador between 1800 and 2350 m.

Phenology.—Flowers and fruits collected in April and December.

Columnea bivalvis is unique among the species of *Columnea* by having a pair of large pendent bracts that enclose a single axillary flower (Figs. 1–2). The yellow tubular flowers are almost completely enclosed by the bracts with only the throat extending beyond the bract margins. The bracts in *C. bivalvis* are superficially similar to the *Drymonia hoppii* and *D. affinis*. Although large bracts are common in many *Columnea* species and especially those belonging to the section *Collandra*, no species is known to have large pendent bracts and dorsiventral shoots.

Columnea bivalvis is similar to *C. medicinalis, C. albiflora,* and *C.eubracteata*. The latter three species differ by the presence of congested bracts compared to a pair of large pendent bracts (i.e., non-congested) in *C. bivalvis*, and by the prominent bilabiate corolla limbs compared to a nearly actinomorphic corolla limb in *C. bivalvis*.

Etymology.—The new species is named in reference to the marine and freshwater mollusca belonging to the class Bivalvia because of the resemblance to the two large rounded bracts that enclose a single axillary flower.

Paratype: **ECUADOR. Napo:** Km 40 from El Carmelo on road towards La Bonita, near 5 km below La Alegría, 0°35'N, 77°30'W, 2350 m, 8 Apr 1979, *B. Lojtnant et al. 11930* (NY).

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BOOK REVIEW

Mahendra Rai, Deepak Acharya, and Jose Luis Rios (eds.). 2011. **Ethnomedicinal Plants: Revitalization of Traditional Knowledge of Herbs.** (ISBN 978-1-57808-696-2, hbk.). Science Publishers, P.O. Box 699, Enfield, New Hampshire 03748, U.S.A.; marketed and distributed by CRC Press, 6000 Broken Sound Parkway, NW, Suite 300, Boca Raton, Florida 33487, U.S.A. (**Orders:** http://www.crcpress.com/ecommerce_product/product_detail.jsf?isbn=9781578086962; www.scipub.net).$129.95, 504 pp., 11 color plates, 6⅛" × 9¼".

Edited by Mahendra Rai, Deepak Acharya, and Jose Luis Rios, *Ethnomedicinal Plants: Revitalization of Traditional Knowledge of Herbs*, consists of 17 chapters from such diverse locales as Mexico, Brazil, West Indies, Lebanon, Nepal, India, Costa Rica, Tunisia, Cameroon, Norway, and Spain. The book markets itself toward "botanists, medicos, Ayurvedic experts, traditional healers, pharmacologists, and common people" interested in the curative properties of healing herbs.

The faults with this book are many and profound. Usually, an edited volume is a result of meetings by international symposia or a single editor's vision, elaborated on by handpicked authors. This volume simply seems to be a disparate collection of papers that have a common keyword: ethnomedicinal. Not surprisingly, this volume does not include an introduction outlining the books mission. Rather, what the reader is presented with here are 17 review papers that look at pharmacology, traditional economic botany of medicinal plants (e.g. an inventory of ethnomedicinal plants in Tunisia), plants for treating specific ailments (e.g. digestive) or action (e.g. anti-inflammatory, immunomodulators), and some interesting anthropological studies (e.g. women's knowledge of herbs used in reproduction). The book closes with an obligatory chapter on the conservation of ethnomedicinal plants and a look at utilizing informatics in ethnobotanical drug discovery. This edition would have been well served to divide these papers in common topical sections (e.g. pharmacology, ethnobotany), or at the very least, order the papers to maintain a tighter thread of continuity.

As an ethnobotanist, I wondered if the books premise, a "Revitalization of Traditional Knowledge of Herbs," was even relevant today. With an aim to "bolster scientific interest in ethnomedicine, leading to an increase in its therapeutic potential in healthcare and medicine," I instantly wondered if this edition was originally published 10 or more years ago (it was not). To say that the literature of medical ethnobotany is copious is no understatement. In fact, the literature on the ethnomedical knowledge of indigenous peoples and the efficacy of some of their medicinal plants is plenty. "Revitalization" in this field seems like a pre-emptive strike, not a scientific endeavor reaching critical mass.

This book was published in a vacuum of its own idealism, written from a laboratory, not a field site. Topical papers addressing intellectual property rights, community involvement and cooperation, and the persistence of ethnomedical knowledge in communities facing western acculturation are either completely ignored or given scant lip-service. And these are the very obstacles that must be overcome to spark revitalization in the field. For a hardback book priced above $100, there is nothing here worthy of an individual purchase. However, it will likely appear in academic libraries holding large collections of pharmacology, phytochemistry, and botanical literature.—*Kevin Janni, Botanist, SWCA Environmental Consultants and BRIT Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

COLUMNEA LUCIFER (GESNERIACEAE), A NEW SPECIES FROM NORTHWESTERN ECUADOR

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ABSTRACT

Recent expeditions to the northwestern slopes of the Ecuadorian Andes and revisionary work of *Columnea* (Gesneriaceae) have resulted in the discovery of a new plant species. The new species, **Columnea lucifer,** is distinguished from other congeners by the presence of dense villous indument on the stems, bright white calyces with red lobes, and elongate tubular yellow corollas with red lobes.

RESUMEN

Expediciones recientes a la vertiente oriental de los Andes Ecuatorianos y el trabajo de revisión del género *Columnea* (Gesneriaceae) permitieron el descubrimiento de una especie nueva de planta. La nueva especie, **Columnea lucifer,** se distingue por la presencia de un denso indumento velloso en los tallos, cáliz blanco lustroso con lóbulos rojos, y corola alargada, tubular, amarilla con lóbulos rojos.

Key Words: *Columnea*, Gesneriaceae, Ecuador, Taxonomy, Flora of Ecuador

INTRODUCTION

The genus *Columnea* is primarily epiphytic and belongs to the New World subfamily Gesnerioideae. *Columnea* is distinguished from other closely related genera by the presence of an indehiscent berry instead of a fleshy bivalved capsule. *Columnea* is the most diverse genus in the subfamily Gesnerioideae with over 200 species (Skog & Boggan 2006; Weber 2004; Burtt & Wiehler 1995). The traditional sectional classification of *Columnea* does not represent monophyletic lineages (Smith 1994; Smith & Sytsma 1994; Clark et al. 2006) and a revised classification system based on molecular sequence data is currently in preparation by the author, James F. Smith, and other collaborators. The species described here is not assigned to any of the traditional subgenera or sections.

TAXONOMIC TREATMENT

Columnea lucifer J.L. Clark, sp. nov. (**Figs. 1, 2**). Type: ECUADOR. Esmeraldas: Cantón San Lorenzo, remnant patch of forest along highway Ibarra-San Lorenzo, between the towns of Durango and Alto Tambo, 00°57'21"N, 78°33'38"W, 664 m, 3 Jun 2009, *J.L. Clark & Gesneriad Research Expedition Participants 11100* (holotype: US; isotypes: QCNE, NY).

A ceteris *Columneae* speciebus indumento dense villoso in caule, calyce vivido candido lobis rubris, et lutea corolla elongatotubulosa lobis rubris differt.

Epiphyte, suffrutescent to herbaceous, stem erect (not scandent), 15–30 cm tall, dense reddish indument throughout, internodes 1.5–4 cm long. **Leaves** opposite, strongly anisophyllous to nearly isosophyllous in a pair, chartaceous; larger leaf with petioles 0.5–1.0 cm long, densely reddish villous indument; blade narrowly oblong to ovate, 9.0–11 × 3.0–4.0 cm, base asymmetrical, apex acute, margin serrate and red; adaxially green, sparsely golden villous; abaxially green with prominent secondary red venation, uniformly villous, 3–6 pairs of lateral veins; smaller leaf variable, nearly equal in size or greatly reduced and stipule like. **Inflorescence** epedunculate with 1–5 flowers per node, bracts narrowly lanceolate, densely villous and red, 5.0 × 0.3 mm, pedicel 1.0–2.5 cm long, red, densely villous and red. **Calyx** bright white with reflexed red lobes; lobes 5, nearly free joined only at the base by 1 mm of their length; 4 lobes equal in size, ovate, 1.0 × 0.5 cm, margin serrate with 4–8 serrations on each side, outside densely villous and white, inside glabrous at base and densely villous at apex, the fifth dorsal lobe smaller, broadly oblong to lanceolate, 0.8 × 0.2 cm.

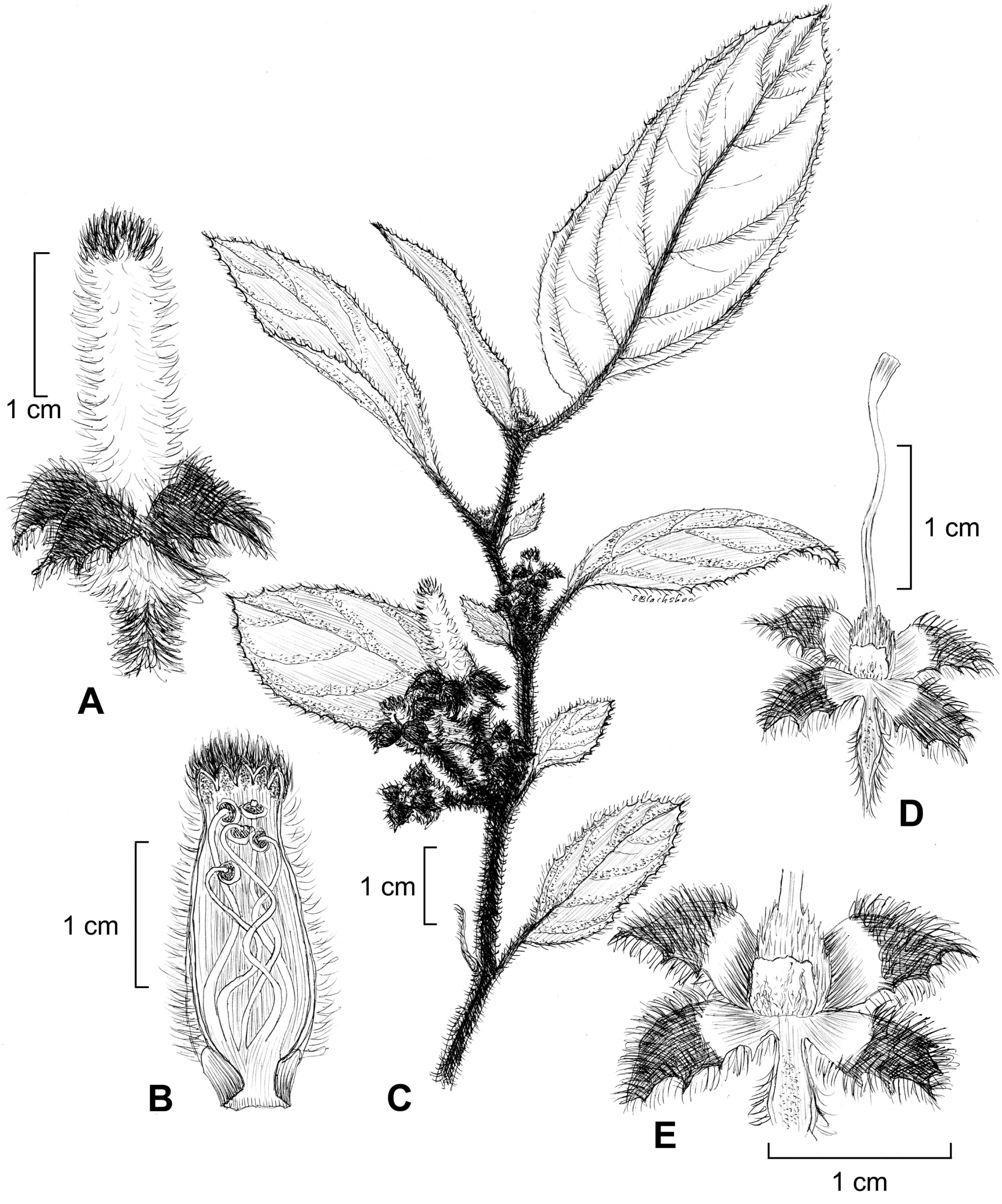

Fig. 1. ***Columnea lucifer*****. A. Mature flower. B. Corolla open to show protandrous stage of mature flower. C. Habit and inflorescence. D. Corolla removed to show calyx, dorsal nectary gland, and immature gynoecium. E. Enlargement of mature calyx.**

Corolla mostly yellow with red apex, uniformly tubular, 2.0–3.0 × 0.5 cm, corolla posture erect in calyx, apical region red, lobes triangular, ca., 1.5 × 2 mm, nearly actinomorphic, outside densely villous, inside glabrous. **Androecium** of 4 stamens, didynamous, included; filaments 1.5–2.0 cm long, basally connate for 3.5 mm, adnate to the base of the corolla tube, glabrous; anthers broader than long, ca. 1.5 mm long, ca. 2.0 mm wide, dehiscing by longitudinal slits; staminode not observed. **Nectary** a single dorsal truncate

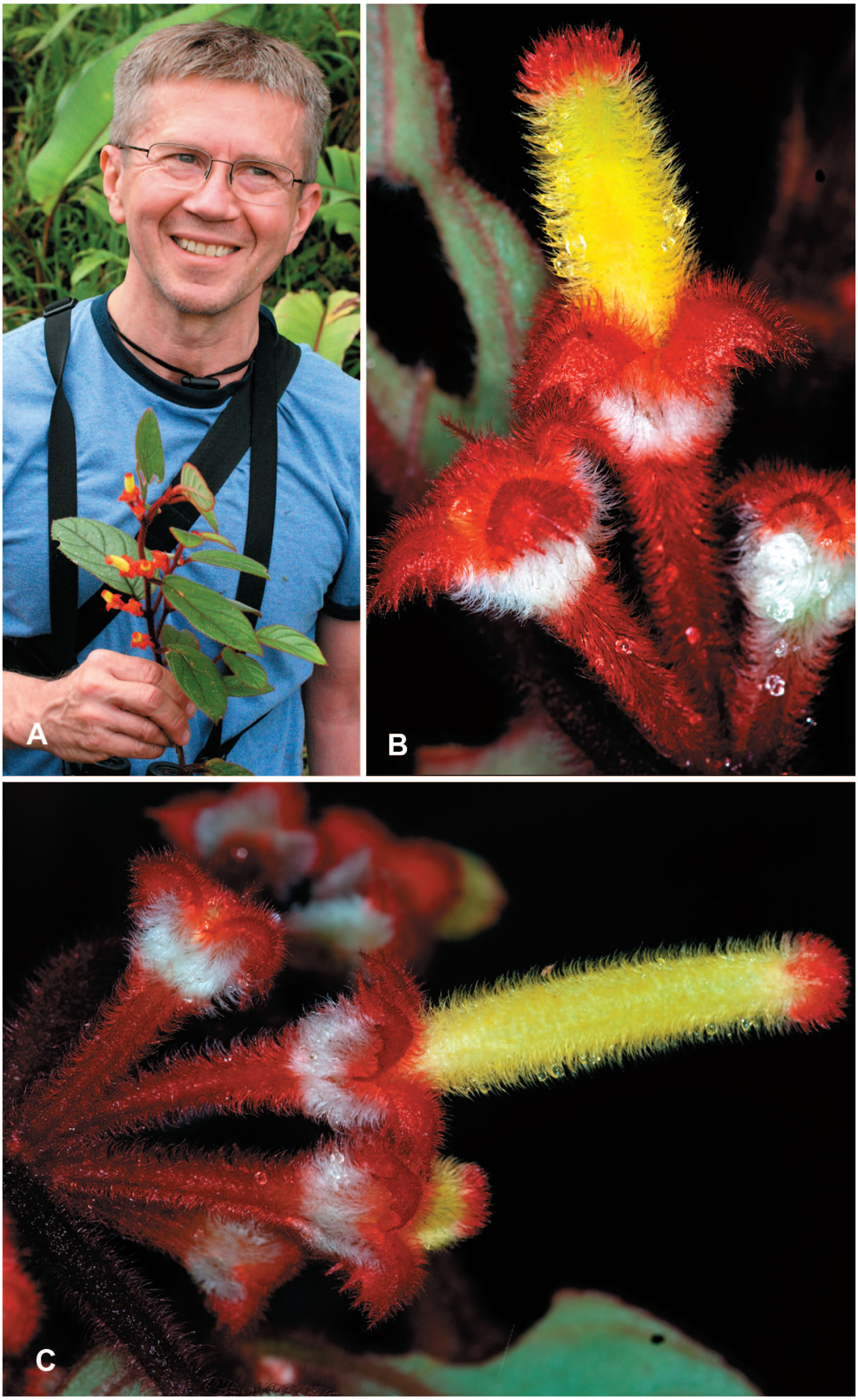

Fig. 2. *Columnea lucifer*. **A.** Stephen Maciejewski holding shoot of entire plant. **B.** Immature flower. **C.** Mature flower. (photo A. by Julie Mavity-Hudson. Photos B & C by J.L. Clark; from the live plant from which the holotype was collected, *J.L. Clark & Gesneriad Research Expedition Participants 11100*).

gland. **Gynoecium** immature, ovary superior, ovoid, 0.7 × 0.3 cm, sericeous; style 1.5–2.0 cm long, laminar; stigma truncate. **Fruit** not observed.

Distribution and habitat.—*Columnea lucifer* is only known from the type locality in a wet forest of northwestern Ecuador. Recent fieldwork in Ecuador with participants on the 2009 Gesneriaceae Research Expedition resulted in the collection of this remarkable species. The group participant who discovered this species is Stephen Maciejewski, an avid and passionate horticulturaist from Philadelphia (Fig. 2A). It is notable that four expeditions conducted by the author to this specific locality and numerous expeditions by other botanists (e.g., Tom Croat and Carlos E. Cerón M.) to the same forest did not result in additional collections of *Columnea lucifer.* It is because of Stephen Maciejewski's acute awareness that this species was discovered.

Recent visits to Ecuadorian herbaria (e.g., Q, QAP, QCA, and QCNE) and many non-Ecuadorian herbaria have not revealed additional collections of *Columnea lucifer.* The only population of *Columnea lucifer* is known from a remnant patch of primary forest along the San Lorenzo-Ibarra highway between the towns of Alto Tambo and Durango. It is noticeable from extensive fieldwork between 2003 and 2009 that most of the forest along the San Lorenzo-Ibarra highway has been converted to African Palm plantations. The habitat from this area is transitional between lowland and montane wet forest. These forests have been classified as *bosque siempreverde piemontano* (Sierra 1999); *selva ombrófila noroccidental del pie de cordillera* (Acosta Solis 1968); *bosque muy húmedo premontano* (Cañadas 1983); and *bosque lluvioso montano bajo* (Harling 1979).

Columnea lucifer is unique among the species of *Columnea* by the dense villous indument on the stems, bright white calyces with red lobes, and elongate tubular yellow corollas with red lobes (Fig. 2). The combination of colors on the pedicel, calyx, and corolla are visually attractive. The colors shift from bright red at the base of the pedicel to bright white on the calyx with reflexed red lobes which contrasts with an elongate corolla that is mostly yellow with strikingly contrasting red apices (Fig. 2).

Etymology.—The new species is named in reference to fire or light-bearer (from the words *lucem ferre*) because of the resemblance of the bright narrow elongate flower with a red apex to a lighted candle with a bright red flame.

ACKNOWLEDGMENTS

Support for this study was provided by the National Science Foundation (DEB-0841958 & DEB-0949169). I thank the Smithsonian Institution's National Museum of Natural History – Department of Botany (US) and Ecuadorian herbaria (Q, QAP, QCA, and QCNE) for access to their collections. I am grateful to James F. Smith (SRP) and an anonymous reviewer for helpful comments on the manuscript, Christian Feuillet for providing the Latin diagnosis, Laura Clavijo for providing the Spanish translation of the abstract, Sue R. Blackshear for preparing the illustration of the new species, William R. Anderson for help in selecting an appropriate specific epithet, and most importantly Stephen Maciejewski for discovering the new species during the 2009 Gesneriad Research Expedition in Ecuador.

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BOOK REVIEW

Ralph W. Tiner, with Abigail Rorer (Drawings). 2009. **Field Guide to Tidal Wetland Plants of the Northeastern United States and Neigboring Canada. Vegetation of Beaches, Tidal Flats, Rocky Shores, Marshes, Swamps, and Coastal Ponds.** (ISBN 978-1-55849-667-5, pbk.; 978-1-55849-666-8, hbk.). University of Massachusetts Press, East Experiment Station, 671 North Pleasant Street, Amherst, Massachusetts 01003, U.S.A. (**Orders:** http://hfs.jhu.edu; hfscustserv@mail.press.jhu.edu; toll-free 800-537-5487). $29.95 (pbk.), $98.00 (hbk.), 416 pp., 570 illustrations, 11 maps, 7" × 10".

As a wetland scientist who has personally used Tiner's *Field Guide to Coastal Wetland Plants of the Southeastern United States* as an indispensible guide to plant identification, I anticipated that this book would possess the same strengths and qualities as its regional counterpart, and without surprise, it does. Designed primarily for readers without training in botany to aid in identifying tidal wetland plants in the northeastern United States and neighboring Canadian provinces, this book is no less valuable to professional and academic botanists and natural scientists.

The books contents include the chapters "Tidal Wetland Types," "Overview of Plant Characteristics," "How to Identify Plants Using this Book," "Keys for Tidal Wetland and Aquatic Plant Identification," "Plant Descriptions and Illustrations," an appendix, "Places to Explore Tidal Wetlands," a glossary, references, and index. More than 700 species are included and for each the author provides a description, flowering and fruiting period, habitat, wetland indicator status, range, and similar species information. On the opposing page, black and white botanical illustrations are provided for one or more of the species. This revised and expanded edition has broadened its coverage both botanically and geographically. More tidal wetland types are included (such as beaches, rocky shores, and tidal swamps) and the geographic scope has expanded to include Canada's Maritime Provinces.

From my own experience with the *Southeastern* field guide, I can imagine this book will be similarly relied upon in the field as an invaluable reference for identifying wetland plants. This expanded edition of the previously definitive book on the subject will encourage those who own the previous edition to upgrade. Tiner is a preeminent wetland scientist and author of five field guides to wetland identification. His experience and hard work is well represented in the pages of this book.

Doubtless, many readers from diverse backgrounds will seek out this is fine update to Tiner's classic book, that was originally published in 1987. It has gained a loyal readership over the years and this edition will surely sustain its well earned reputation. I would recommend this book to botanists and wetland scientists working in the northeastern United States and nearby Canada without hesitation.—*Kevin Janni, Botanist, SWCA Environmental Consultants and BRIT Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

COLUMNEA PYGMAEA (GESNERIACEAE), A NEW SPECIES FROM NORTHWESTERN ECUADOR

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ABSTRACT

Recent expeditions to the northwestern slopes of the Ecuadorian Andes and revisionary work of *Columnea* (Gesneriaceae) have resulted in the discovery of a new plant species. The new species, **Columnea pygmaea,** is distinguished from other congeners by small flowers (< 1 cm), erect shoots, and an obligate epiphytic habit. A discussion that includes a dichotomous key and digital images is presented to provide a better understanding of and to differentiate *Columnea pygmaea* from *C. parviflora*, *C. herthae*, *C. minutiflora*, and *C. lehmannii*.

RESUMEN

Como resultado de las recientes expediciones al noroccidente de los Andes ecuatorianos y del trabajo de revisión del género *Columnea* (Gesneriaceae), se ha descubierto una nueva especie para la ciencia. La nueva especie, **Columnea pygmaea,** se distingue de sus congéneres por tener flores pequeñas (< 1 cm), vástagos erectos, y hábito holoepífito. Además de la descripción de la especie, se presenta una clave dicotómica e imágenes digitales para brindar un mejor entendimiento y diferenciación entre *Columnea pygmaea* de *C. parviflora*, *C. herthae*, *C. minutiflora* y *C. lehmannii*.

Key Words: *Columnea*, Gesneriaceae, Taxonomy, Flora of Ecuador

INTRODUCTION

The genus *Columnea* is primarily epiphytic and belongs to the New World subfamily Gesnerioideae. The genus ranges from Mexico south to Bolivia and is one of the largest genera of the family in the New World tropics with over 200 species. *Columnea* is distinguished from other closely related genera by the presence of an indehiscent berry instead of a fleshy bivalved capsule. *Columnea* is the most diverse genus in the subfamily Gesnerioideae with over 200 species (Skog & Boggan 2006; Weber 2004; Burtt & Wiehler 1995). The traditional sectional classification of *Columnea* does not represent monophyletic lineages (Smith 1994, Smith & Sytsma 1994; Clark et al. 2006) and a revised classification system based on molecular sequence data is currently in preparation by the authors. The species described here belongs to a well-supported clade (Smith et al., in review) that does not yet have a formal designation. Many of the specimens that resemble *Columnea pygmaea* J.L. Clark & J.F. Smith are incorrectly determined in herbaria. Plates of digital images and a key are provided to help differentiate *Columnea pygmaea* from the following morphologically similar species: *Columnea parviflora* C.V. Morton, *C. herthae* Mansf., *C. minutiflora* L.P. Kvist & L.E. Skog, and *C. lehmannii* Mansf.

TAXONOMIC TREATMENT

Columnea pygmaea J.L. Clark & J.F. Smith, sp. nov. (**Fig. 1**). Type: ECUADOR. Esmeraldas: Cantón San Lorenzo, remnant patch of forest along Highway Ibarra-San Lorenzo, between the towns of Durango and Alto Tambo, 1°01'22"N, 78°36'30"W, 460 m, 3 Jun 2009, *J.L. Clark & Gesneriad Research Expedition Participants 11180* (holotype: US; isotypes: BRIT, CAS, K, MO, NY, QCNE, SEL, UNA).

A *Columnea herthae* corollis minus quam 1 cm longis vice 2 cm, caulibus erectis vice pendentium differt.

Obligate epiphytic herb, roots fibrous, stems erect (not scandent), 7–20(–40) cm tall, sparsely villous throughout, internodes 1–4 cm long. **Leaves** opposite, subequal to strongly unequal in a pair; larger leaf with petioles 0.5–1.5 cm long, villous; blade elliptic to narrowly ovate, 2.0–7.0 × 1.5–3.5 cm, base asymmetrical, apex acute to obtuse, margin shallowly serrate to crenate; adaxially bright green, sparsely villous; abaxially

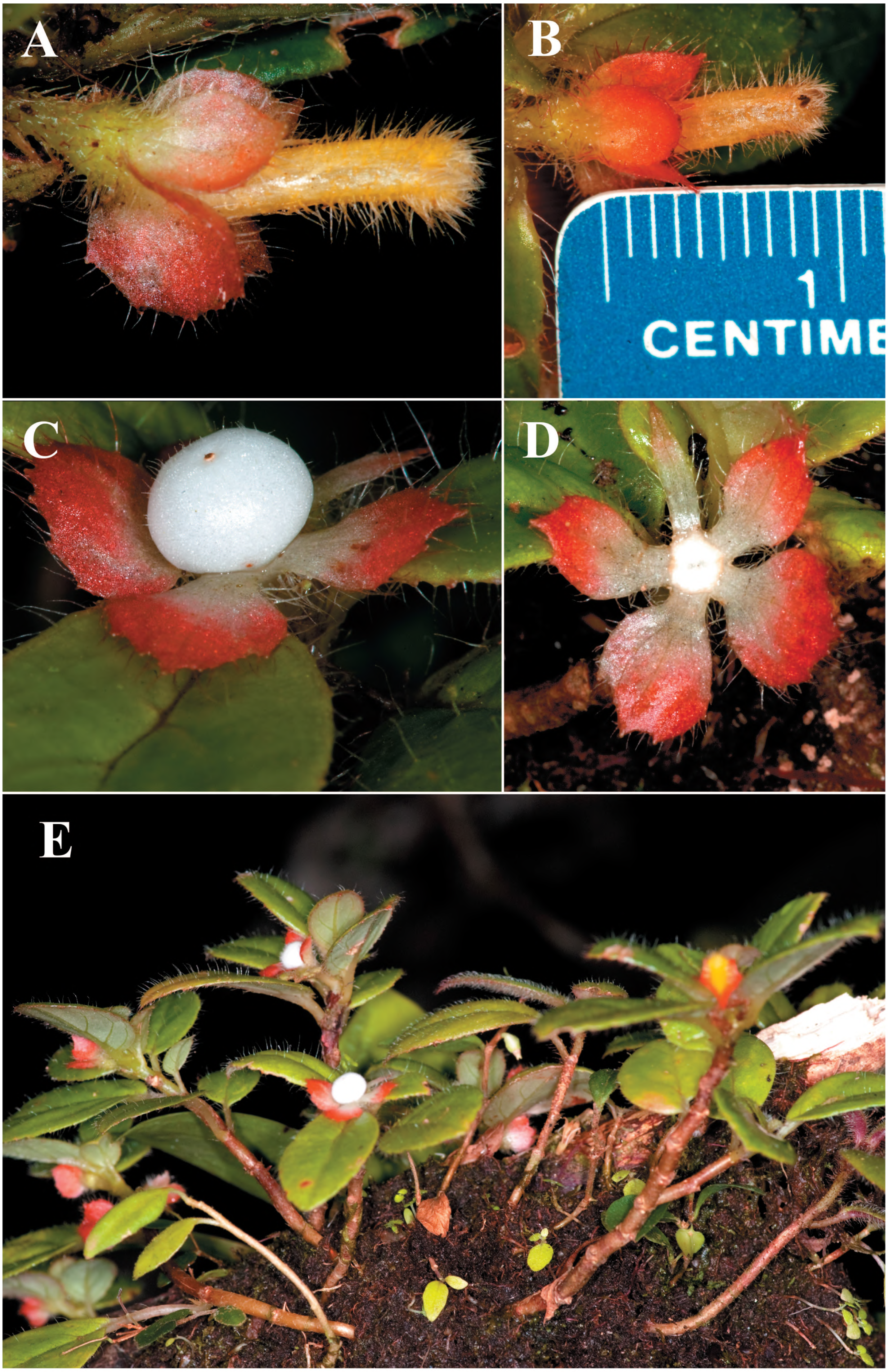

Fig. 1. ***Columnea pygmaea*****. A & B.** Mature flower. **C.** Mature berry. **D.** Berry removed to show calyx. **E.** Habit (Photos by J.L. Clark from the field collection of the holotype, *J.L. Clark & The Gesneriad Research Expedition Participants 11180*).

greenish-white, sparsely to densely villous (especially on veins), 3–4 pairs of lateral veins; smaller leaf similar to larger leaf, but greatly reduced, 0.5–1.5 × 0.2–0.5 cm. **Inflorescence** reduced, epedunculate and appearing fasciculate with 1–3 flowers per node, bracts persistent, 0.2 × 0.1 cm, bright red; pedicel 0.3–0.5 cm long, villous to densely villous near base of calyx and red. **Calyx** bright red with reflexed red lobes at anthesis; lobes 5, nearly free; 4 lobes equal in size, ovate to broadly ovate, ca., 0.5 × 0.5 cm, margin with 3–5 serrations on each side, sparsely villous near apex and densely villous at base, inside sparsely villous, the fifth dorsal lobe smaller, lanceolate, 1.0 × 0.2 cm. **Corolla** pale yellow, tubular, 0.7–0.9 × 0.2–0.3 cm, corolla posture erect in calyx, lobes erect, white to pale-yellow, limb nearly actinomorphic, outside sparsely villous near base to densely villous near apex, inside glabrous. **Androecium** of 4 stamens, didynamous, included; staminode not observed. **Nectary** a single dorsal truncate gland. **Gynoecium** immature, ovary superior, ovoid. **Fruit** an indehiscent white berry, appearing dorsally flattened, 0.5 cm in diameter.

Distribution and habitat.—*Columnea pygmaea* is known from two collections from wet forests along the western slopes of the Ecuadorian Andes. The first collection of *Columnea pygmaea* was by Hans Wiehler and Calaway Dodson (*H. Wiehler & C.H. Dodson 7113*) from the province of Pichincha (Rio Baba, Hwy Santo Domingo-Quevedo). Additional collections since the early 1970s are from cultivated material that was distributed from Cornell University's L.H. Bailey Hortorium. The cultivated material apparently originated from Wiehler and Dodson's 1971 field collection.

The tropical wet and moist coastal forests of western Ecuador below 1000 meters once encompassed a band from Colombia to Peru that reached a maximum width near the northern limit and was very narrow and broken to the south. Dodson and Gentry (1991) estimated that while this forest type once covered 15% of western Ecuador, currently less than 0.8 % of the coastal wet and moist forests remain. It is not surprising that *Columnea pygmaea* has not been recollected since 1971 because of the near eradication of this forest type from western Ecuador. The endemism of the flowering plant family Gesneriaceae in western Ecuador is estimated at 20%, which is significantly higher than the 12% endemicity reported for western lowland Ecuador (defined as below 1000 m) as reported by Jørgenson and León-Yánez (1999) and Valencia et al. (2000). The endemicity of the Gesneriaceae in western Ecuador is especially important for evaluating conservation priorities because at least 20 of the 23+ species were evaluated and considered extinct or endangered by Kvist et al. (2004) according to the IUCN Red List categories (IUCN 2001).

Fieldwork in Ecuador with participants of the 2009 Gesneriaceae Research Expedition resulted in the discovery of a second population and extension of the species known range into the northern Ecuadorian province of Esmeraldas. The type locality of *Columnea pygmaea* is from a remnant patch of primary forest along the San Lorenzo-Ibarra highway between the towns of Alto Tambo and Durango at 460 m. It was noticed by the first author during extensive fieldwork between 2003 and 2009 that most of the forest along the San Lorenzo-Ibarra highway had been converted to African Palm plantations. The original habitat from this area is transitional between lowland and montane wet forest. These forests have been classified as *bosque siempreverde piemontano* (Sierra 1999); *selva ombrófila noroccidental del pie de cordillera* (Acosta Solis 1968); and *bosque lluvioso montano bajo* (Harling 1979).

Discussion of circumscription.—*Columnea pygmaea* is unique among the species of *Columnea* by the short corollas that are less than 1 cm in length (Fig. 1B). *Columnea parviflora* consistently has corollas that are less than 1 cm in length (Fig. 2A), but the habit and calyx margin help differentiate this species from *C. pygmaea*. The pendent and climbing habit of *C. parviflora* (Fig. 2E) helps differentiate it from the erect stems and non-climbing habit of *C. pygmaea* (Fig. 1E). The calyx lobes of *Columnea parviflora* are fimbriate (Fig. 2C–D) in contrast to the shallow serrations in *C. pygmaea* (Fig. 1D). Both *Columnea pygmaea* and *C. herthae* have uniformly pale-yellow tubular corollas with four equal calyx lobes and one (dorsal) lobe that is reduced and lanceolate (Fig. 1D & Fig. 3C). In contrast to four equal calyx lobes with one reduced calyx lobe, *Columnea minutiflora* (Fig. 4) and *C. parviflora* (Fig. 2) have five calyx lobes that are nearly equal in size and shape.

The above three species are common in northwestern Ecuador and southern Colombia. In contrast,

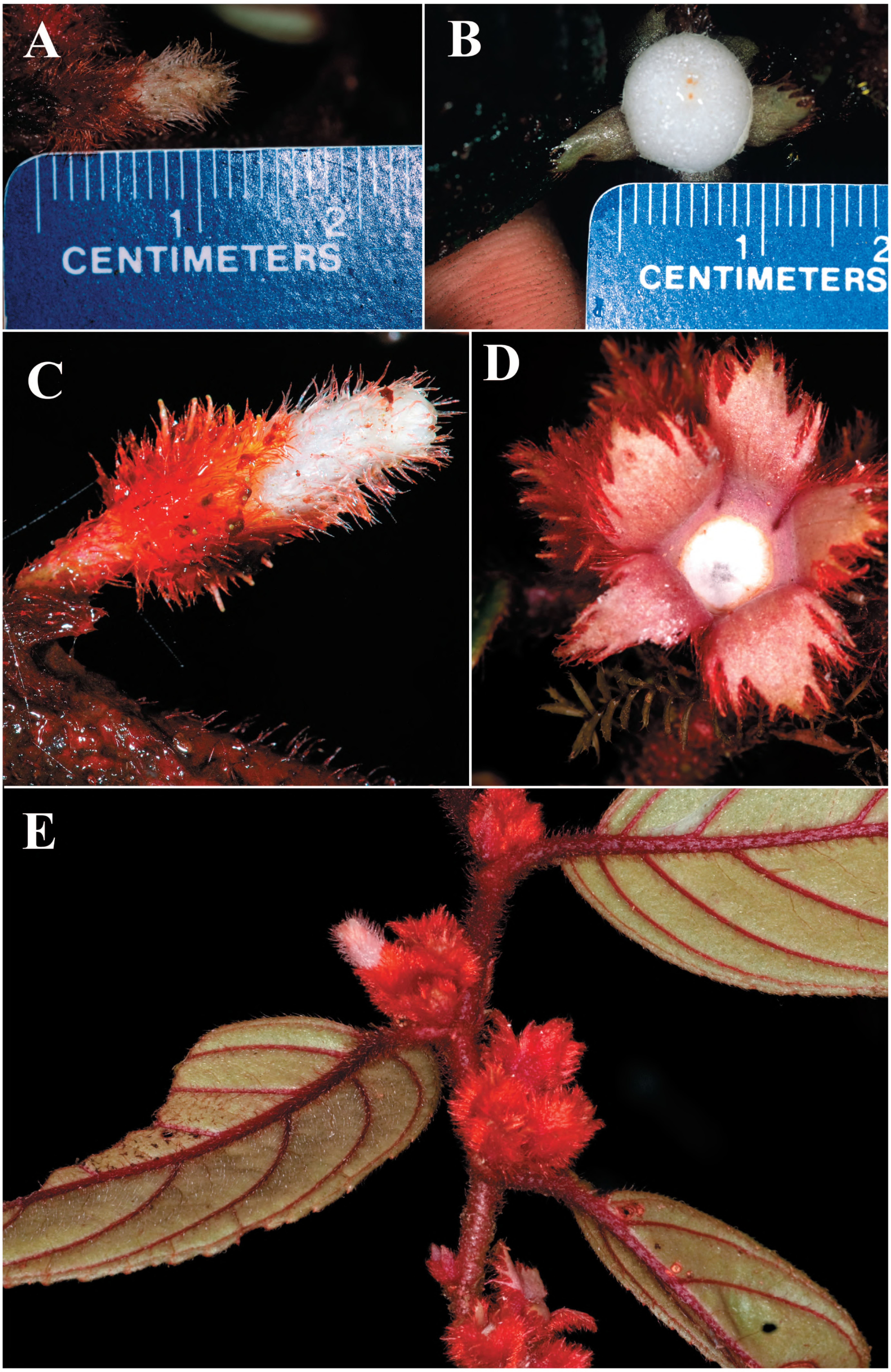

Fig. 2. *Columnea parviflora*. **A.** Mature flower. **B.** Mature berry. **C.** Mature flower. **D.** Berry removed to show calyx. **E.** Habit (Photos by J.L. Clark, A & B *J.L. Clark, R. Fleiss & I. Salinas 8817*, C. *J.L. Clark & The University of Alabama in Ecuador Program Participants 9644*, D & E. *J.L. Clark & The University of Alabama in Ecuador Program Participants 10832*).

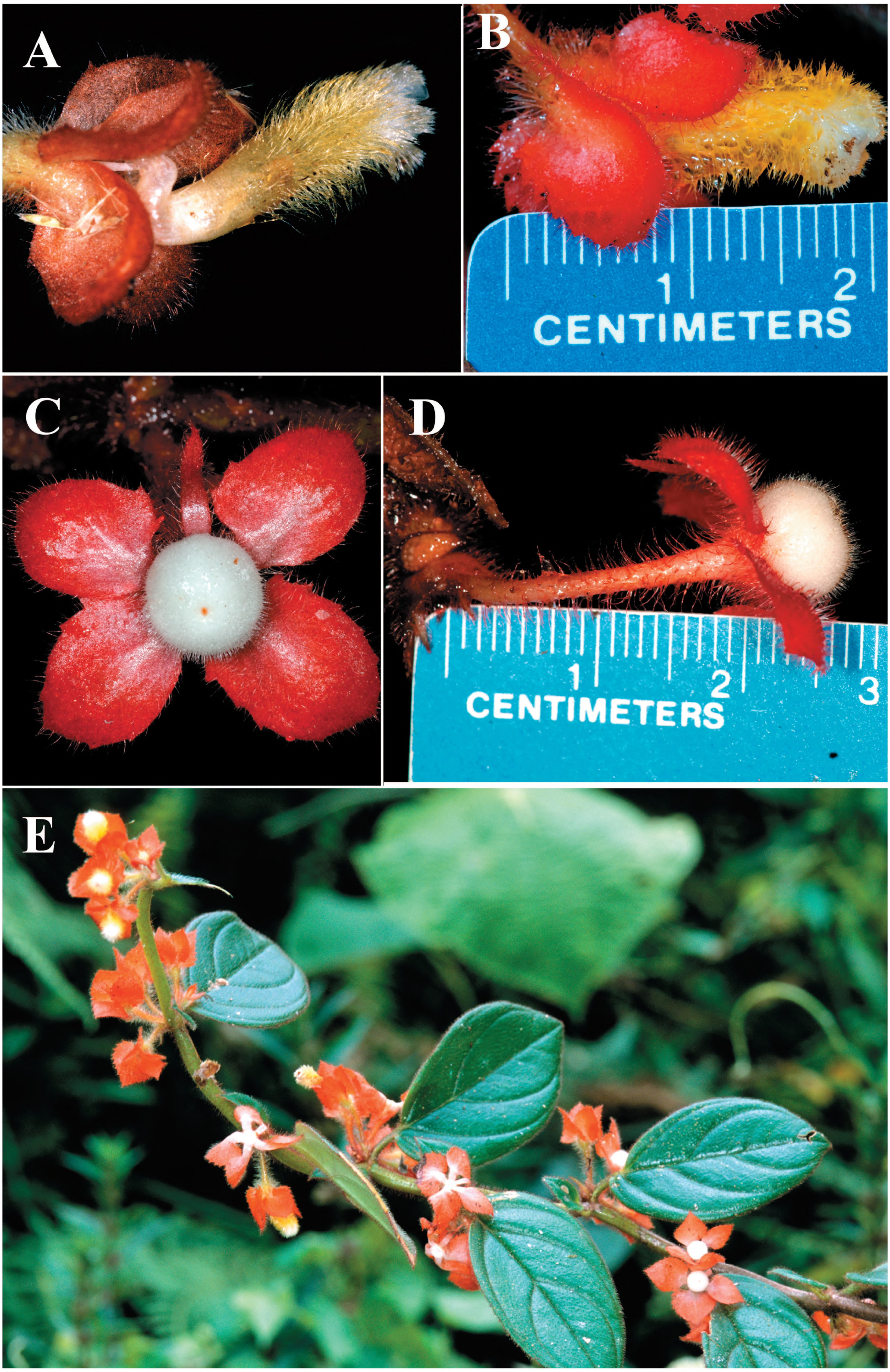

Fig. 3. Columnea herthae. **A & B.** Mature flower. **C & D.** Mature berry. **E.** Habit (Photos by J.L. Clark, A, B & E, J.L. Clark, G. Zapata & G. Toasa 7113, C & D. *J.L. Clark & The Gesneriad Research Expedition Participants 11193*).

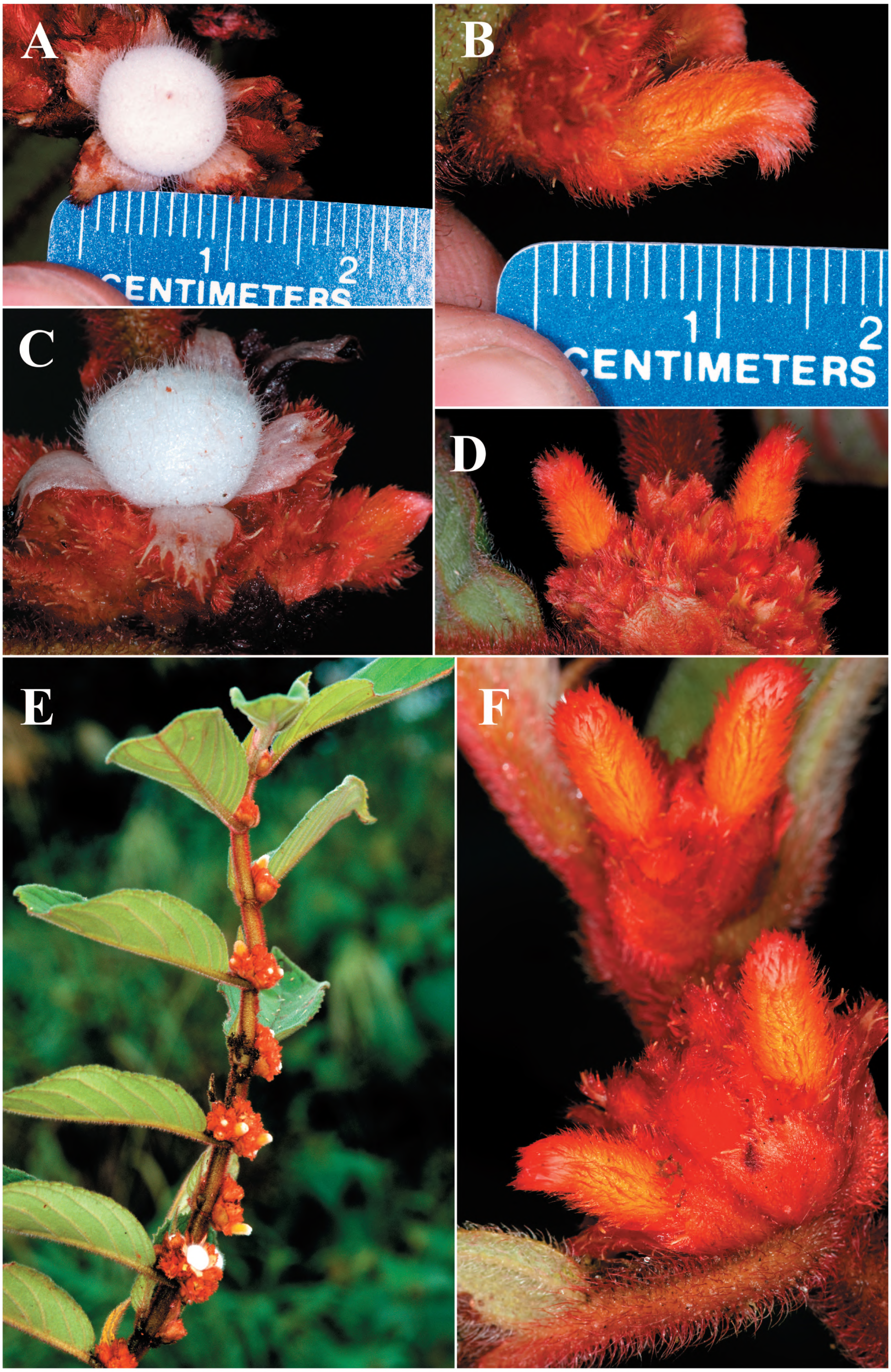

Fig. 4. *Columnea minutiflora*. **A.** Dorsal view of mature berry. **B.** Mature flower. **C.** Lateral view of mature berry. **D.** Inflorescence. **E.** Habit. **F.** Inflorescence (Photos by J.L. Clark, A, *J.L. Clark 7092*, B. & D. *J.L. Clark & The Gesneriad Research Expedition Participants 11091*, C. & F. *J.L. Clark & The Gesneriad Research Expedition Participants 11132*, E. *J.L. Clark 7200*).

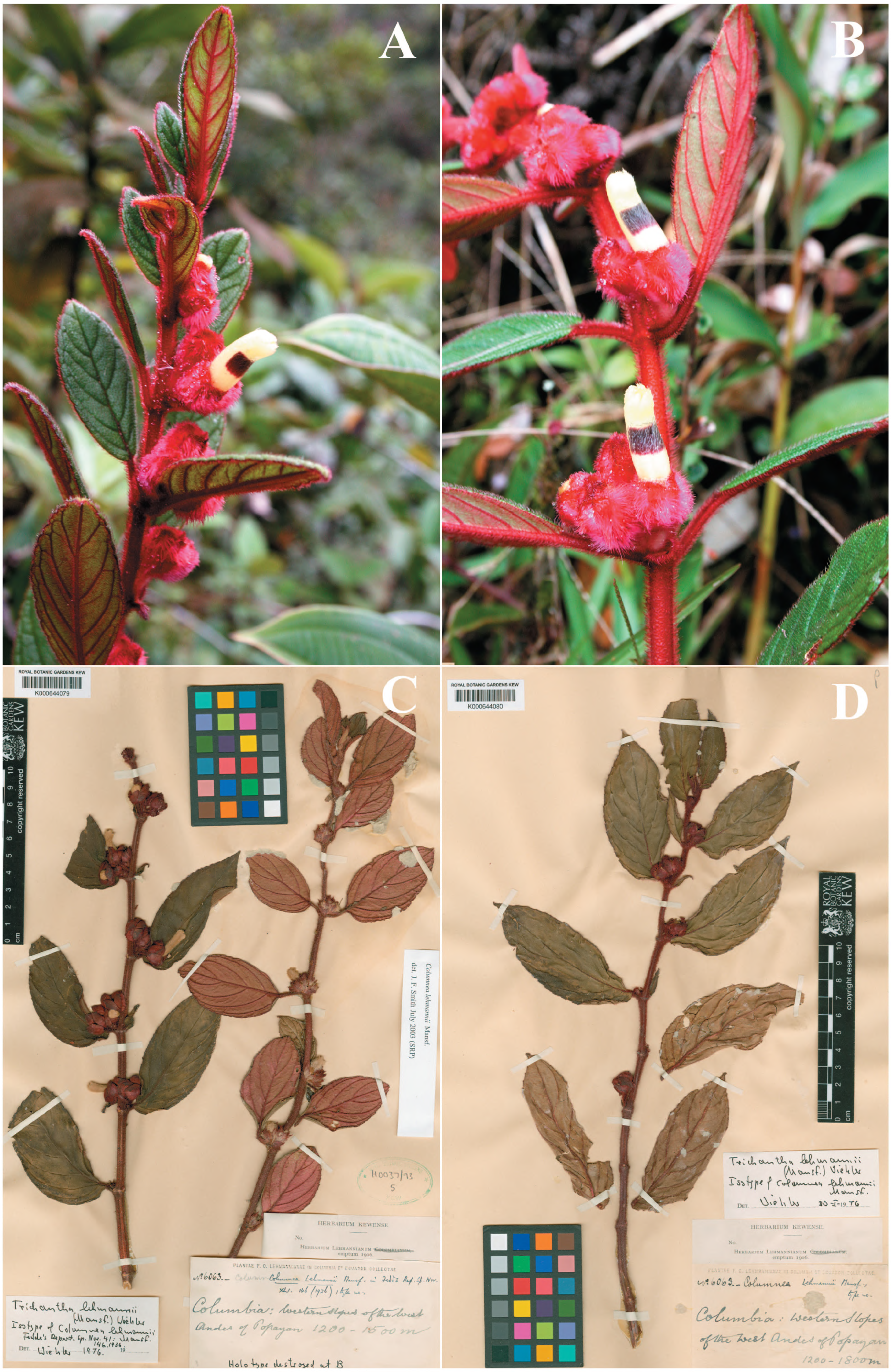

Fig. 5. *Columnea lehmannii*. **A. & B.** Habit with erect inflorescence. **C.** Lectotype of *C. lehmannii*, *F. Lehmann 6063* (K). **D.** Isolectotype of *C. lehmannii*, *F. Lehmann 6063* (K). (Photos A & B. by J. Betancur of *J. Betancur et al. 12359* from the Parque Nacional Tatamá, C. & D. Specimens from the Royal Botanic Gardens, Kew).

Columnea lehmannii is common in Colombia, but is known from Ecuador by a single collection (*Kvist et al. 48983*, AAU), which has not been seen by the authors of this study. Confusion between *Columnea lehmannii* and other species discussed here is evident from many misidentified collections at MO, NY, QCA, QCNE, SEL, and US. Many herbarium collections previously identified as *Columnea lehmannii* clearly belong to *Columnea herthae* (e.g., the 25+ collections made and distributed by the first author to numerous herbaria). *Columnea lehmannii* is differentiated by the presence of larger corollas (> 2 cm long; Fig. 5 A & B). The presence of opposite leaves that are nearly equal in size is rare in other species and relatively common in *C. lehmannii* (Fig. 5), but occasionally the opposite leaves are strongly anisophyllous (Fig. 5 D).

Etymology.—The new species is named in reference to the small stature of the plants. The flowers of *Columnea pygmaea* (Fig. 1B) are similar in shape to *Columnea herthae* (Fig. 3B), but differ by their significantly smaller size.

Conservation and IUCN Red List category.—*Columnea pygmaea* has not been found in any formally protected area in Ecuador. According to the IUCN Red List criteria (IUCN 2001) for limited geographic range (B2a, less than 10 km^2 and known to exist at only a single location) and considering the uncertain future of habitat conservation along the San Lorenzo-Ibarra highway, *Columnea pygmaea* should be listed in the category CR (Critically Endangered).

Paratypes.—**ECUADOR. Pichincha:** Rio Baba (=Rio Quevedo, Rio Palenque), km 7 on road from Santa Domingo to Quevedo, 21 Jul 1971, *H. Wiehler & C.H. Dodson 7113* (=Wiehler live accession W-1573) (US); cultivated collection from L.H. Bailey Hortorium of *H. Wiehler & C.H. Dodson 7113*, 7 Jan 1975, *M.H. Stone 1305* (SRP, US).

KEY TO THE COMMON SPECIES OF *COLUMNEA* WITH CRENATE-MARGINED OBLONG LEAVES

1. Calyx margins deeply fimbriate ____ **Columnea parviflora**
1. Calyx margins serrate to entire
    2. Reduced inflorescence of 1–3 flowers with well-developed pedicels
        3. Corolla less than 1 cm long, stems less than 40 cm tall ____ **Columnea pygmaea**
        3. Corolla 1.5 – 2.0 cm long, stems more than 40 cm tall ____ **Columnea herthae**
    2. Reduced inflorescence of 4–6 flowers with each flower appearing sessile
        4. Corolla 1–1.5 cm long, corolla uniformly colored and lacking markings ____ **Columnea minutiflora**
        4. Corolla 2.0 to 4 cm long, corolla not uniformly colored, tube with broad red band on ventral surface ____ **Columnea lehmannii**

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BOOK REVIEWS

James H. Everitt, D. Lynn Drawe, Christopher R. Little, and Robert I. Lonard. 2011. **Grasses of South Texas: A Guide to Identification and Value.** (ISBN 978-0-89672-668-0, pbk.). Texas Tech University Press, Box 41037, Lubbock, Texas 79409-1037, U.S.A.). (**Orders:** www.ttupress.org; 800-832-4042). $49.95, 446 pp., 300 color photos, 6 illustrations, 1 map, 6" × 9".

This is another fine edition of the Grover E. Murray Studies in the American Southwest series by Texas Tech University Press. Like other recent titles in the series, such as *Plants of Central Texas Wetlands* by Fleener and Taber (2009), and *Trees, Shrubs, and Cacti of South Texas* by Drawe and Lonard (2002), this edition also serves as an excellent field guide and general reference for specialists and non-specialists alike. This edition on the grasses of south Texas covers the South Texas Plains and Coastal Prairies and Marshes vegetational areas and includes more than 30 counties that occupy nearly 23,000,000 acres.

The contents include an introduction, a key to the genera of grasses of south Texas plains and adjacent coastal prairies and marshes, a description of the grasses, a glossary, literature cited, and an index. Users of this book will appreciate the extremely well produced close-up photography of each species that were obtained by scanning pressed vouchers at a high resolution. These close-ups of the spikelets and inflorescences for each species make the book considerably more useful had they been black and white illustrations or general photography of uneven quality. Habitat and habit photographs are only included for some species. For each species, Latin and common names, and descriptive information is given; as well as, its relative importance to livestock, wildlife, and people. In all, 250 taxa in nine subfamilies, 15 tribes, and 88 genera are treated. These species include 175 native species and 75 that were introduced. Despite its focus on the southern tip of Texas, it will likely be referenced for others areas of the state, the American Southwest and Great Plains, and northern Mexico.

Grasses of South Texas will soon be added to the libraries of botanists and naturalist of Texas, particularly, south Texas. Not only does it encompass a wide range of common and uncommon species, its aid in actual plant identification is greatly enhanced by the high-resolution scans of pressed field samples. These images show details of plant parts that are too often absent from the majority of similar books. Further, they serve well as a field aid as these images are not of dried herbarium specimens, but what appears to be recently pressed field samples. These impressive images may soon set the standard for future botanical identification texts. As a professional and student of Texas botany, I expect to break the binding and dirty the pages of this book the next time I botanize in south Texas.—*Kevin Janni, Botanist, SWCA Environmental Consultants and BRIT Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

Kelby Ouchley. 2010. **Flora and Fauna of the Civil War: An Environmental Reference Guide.** (ISBN 978-0-8071-3688-1, hbk.). LSU Press, 3990 West Lakeshore Drive, Baton Rouge, Louisiana 70808, U.S.A. (**Orders:** www.lsu.edu/lsupress/orderingInfo.html; customerservice@longleafservices.org; toll free 800-848-6224). $29.95, 7 halftones, 6" × 9".

In an unusual blend of botany, history, and humanity, Kelby Ouchley has produced a fascinating, illuminating, and historically accurate account of the Civil War, the people who were directly or indirectly involved, and the ultimate environmental aftermath. Citing a contemporary, he wrote, "More than three decades of accumulated literature in environmental history barely touch the Civil War" (J.T. Kirby, 2001; 2009). A trained biologist, Ouchley worked for over thirty years as manager of the national wildlife refuges for the U.S. Fish and Wildlife Service. He has the training and experience, and he has done an excellent job of correcting that omission.

Part 1 deals with the flora of the area and Part 2, the fauna. Vernacular terms are used for headings; scientific terms (usually in parentheses) are supplied; and descriptions, common usage, and related information are provided.

The unusual aspect of this volume is the author's use of the many letters among people who were directly or indirectly touched by the Civil War. Following each description were snippets of personal letters between military, family, friends, refugees, etc. These letters (often with the author supplying the proper name, spelling, or explanation in square brackets) capture all the hardships as well as the emotions experienced in warfare—especially in that time period.

Ouchley states, "Within the area impacted by the Civil War, there are no documented cases of historical extinctions of plants or animals before or during the conflict." He discusses various other concerns and possibilities. Events following the Civil War—"new technology and the rush to rebuild the South"—were major factors "in the near total elimination of virgin forests in the eastern United States."

Unfortunately, the challenges are still many and "unprecedented." Partisan factions now rival earlier ones. He concludes, "Only a successful outcome will prevent resource-based wars of the future and their unimaginable environmental consequences."

His final paragraph (following the quotation above): General Robert E. Lee, CSA, in a letter to his wife from Pocahontas County, present-day West Virginia, on Aug. 4, 1861: "I enjoyed the mountains, as I rode along. The views are magnificent--the valleys so beautiful, the scenery so peaceful. What a glorious world Almighty God has given us. How thankless and ungrateful we are, and how we labour to mar His gifts."—*Helen Jeude, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

BEGONIA BERNICEI (BEGONIACEAE), A NEW SPECIES FOR THE LOWLAND HUMID FORESTS OF THE VENEZUELAN GUAYANA

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ABSTRACT

A new species of *Begonia* section *Doratometra*, **B. bernicei,** from the lowland humid forest of the Venezuelan Guayana, is described and illustrated. The new species is similar to *B. semiovata*, but it differs in its larger leaves, petiole, and inflorescence, the tepals of the staminate flowers that are different in shape and size, and the four tepals of the pistilate flowers.

RESUMEN

Se describe y se ilustra una nueva especie de *Begonia* sección *Doratometra,* **B. bernicei,** de los bosques húmedos de tierras bajas de la Guayana Venezolana. Esta nueva especie es similar a *B. semiovata,* sin embargo difiere de esta por poseer las hojas, los pecíolos y las inflorescencias más grandes, los tépalos de las flores estaminadas difieren en tamaño y forma, y las flores pistiladas poseen cuatro tépalos.

INTRODUCTION

The genus *Begonia* was described by Linnaeus (1753) and later circumscribed by Irmscher (1925), Doorenbos et al. (1998), Forrest and Hollingsworth (2003), and Tebbitt (2005). *Begonia* is remarkable because it includes all the species of the family Begoniaceae, except for one species referred to *Hillebrandia sandwicensis* Oliver, which is endemic to Hawaii (Clement et al. 2004). Comprising more than 1500 species (Govaerts 2009), *Begonia* is the sixth largest genus of flowering plants, and it is distributed throughout the tropics and subtropics with the exception of Australia (Frodin 2004; Tebbitt 2005).

Begonia, undoubtedly due to its large size, has been divided into numerous sections. The most recent sectional account is that of Doorenbos et al. (1998), who recognized sixty three sections. Three additional new sections have been described recently (Shui et al. 2002; Forrest & Hollingsworth 2003; de Wilde & Plana 2003). The sections of *Begonia* are recognized based on a combination of morphological features such as leaf venation, perianth segment number, features of the pistillate and staminate flowers, and the shape of the fruits (Nguyen & Tebbitt 2006).

Family treatments were prepared for the *Flora of Venezuela* (Smith & Wasshausen 1989), and the *Flora of the Venezuelan Guayana* (Steyermark 1997), who recognized 47 and 11 species, respectively. In addition, Dorr (1999) reevaluated several taxa from the Venezuela Andes, and recently the family was revised for the "*Catálogo ilustrado y anotado de las plantas de los Llanos de Venezuela*" (Duno et al. 2007) and the "*Nuevo Catálogo de la Flora vascular de Venezuela*" (Hokche et al. 2008). This later contribution increases to forty nine the number of *Begonia* species known from Venezuela, 23 of which are considered endemic.

Herbarium material of the new species described here was first pointed out to the auhors in 1991 by L.B. Smith (1904–1997), a noted bromeliad and *Begonia* taxonomist. Subsequently, the authors found two additional collections, which together provide enough material to describe it.

TAXONOMIC DESCRIPTION

Begonia bernicei Aymard & G.A. Romero, sp. nov. (**Fig. 1**). Type: VENEZUELA. Estado Bolívar: Municipio Sucre, alrededores de Santa María de Erebato, 04°59'N; 64°49° O, 360 m, Feb 1989, *E. Sanoja 2611* (holotype: PORT; isotype: US).

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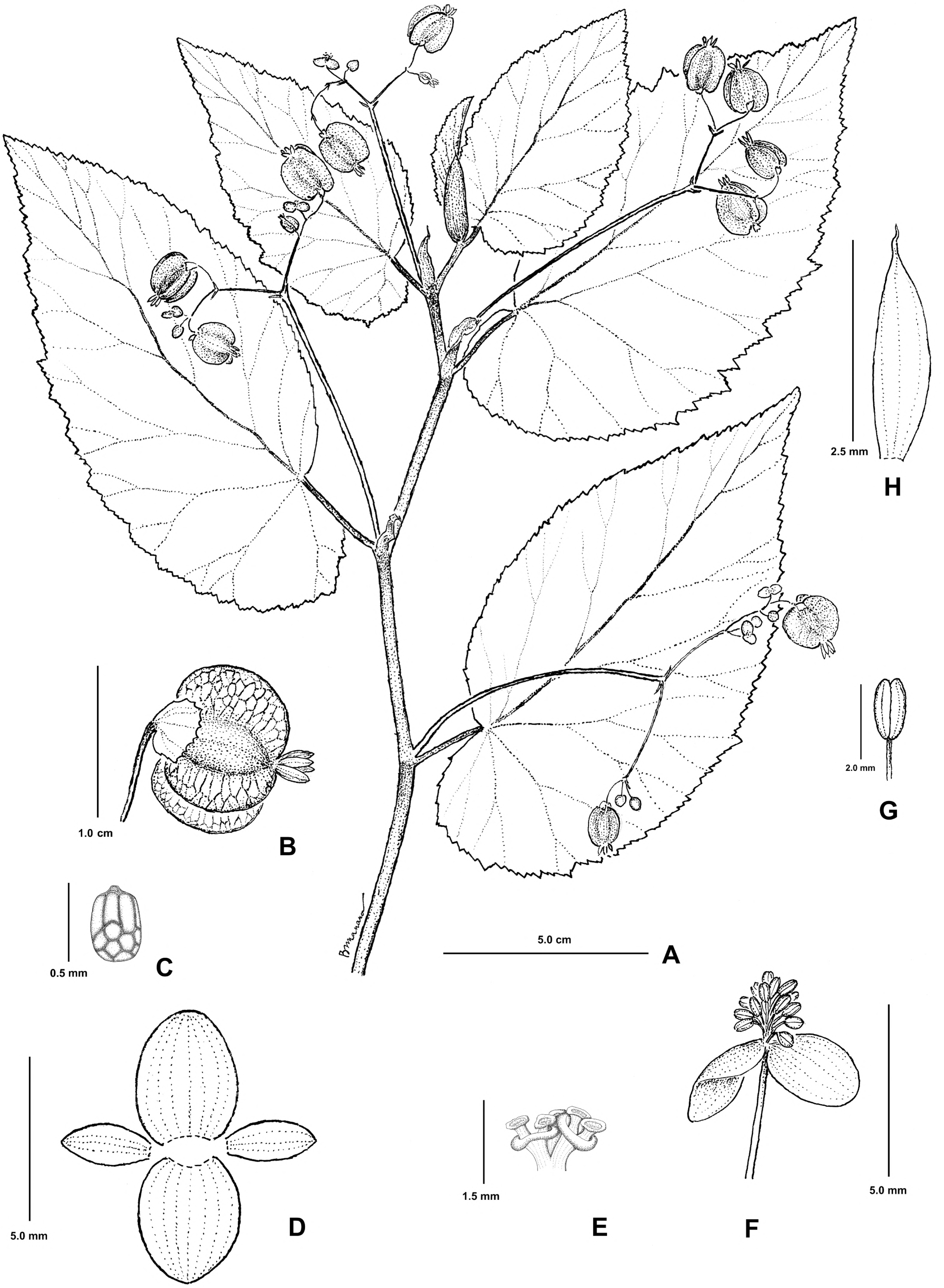

Fig.1. *Begonia bernicei* (A–H from the holotype, *E. Sanoja 2611*, PORT). **A.** Habit; **B.** Fruit; **C.** Seed front view; **D.** Tepals of the pistillate flower; **E.** Bifid styles (the one on the back only partially shown); **F.** Staminate flower; **G.** Stamen; **H.** Stipule. A–B, D, and F–H drawn by Bruno Manara; C and E drawn by Angelina Licata.

Begonia bernicei, sectionis *Doratometra* (Klotzsch) A. DC., et *Begoniae semiovatae* Liebm proxima, sed differt: foliis 7–14 × 4–8 cm, petiolo 2–4 cm longo, inflorescentia axillari et terminali, 6–8 cm longa, tepalis florum staminalium ex orbiculari reniformibus, 3 × 3 mm, tepalis pistillarium florum, 4.

Suffrutescent *herb, stems* 2–5 mm in diameter, green, grooved, glabrous, internodes 3–8 cm long. *Stipules* deciduous, ca. 15 × 6 mm, green, ovate to triangulate, glabrous and reticulate on both surfaces, margins entire, apex with an acumen ca. 2 mm long. *Leaf lamina* 7–14 × 4–8 cm, asymmetric, delicately membranaceous, broadly ovate, glabrous on both surfaces, apex acuminate, base obliquely cordate, margins ciliate-denticulate, venation palmate, main veins 8–9, these red on the lower surface, tertiary veins reticulate, inconspicuous; *petiole* 2–4 cm long, green, glabrous, canaliculate at the base, joining lamina at an ca. 65° angle. *Inflorescence* axillary and terminal, erect, 6–8 cm long, 4–6-flowered, cymose, once dichotomous branched, glabrous, penduncles pink to light green; *bracts* caducous, ovate, 2–3 × ca. 2 mm, glabrous on both surfaces, margins entire, apex acuminate. *Staminate flowers* white; pedicels 3–5 mm long, glabrous, tepals 2, white, orbicular to reniform, 3 × 3 mm, glabrous and reticulate on both surfaces, androphore absent; stamens 25–30, arranged in an actinomorphic cluster, filaments free, 1–1.5 mm long, glabrous, anthers oblong, ca. 1.4 mm long, glabrous, connective projecting; *pistillate flowers* white; pedicel ca. 2 mm long, glabrous; bracteoles caducous, ca. 3 × ca. 4 mm, orbicular, glabrous on both surfaces, margins ciliate-serrulate, tepals 4, glabrous and reticulate on both surfaces, apex obtuse, margins entire, outer pair ovate, 1–2 × 1–1.5 mm; inner pair oblanceolate, 1–3 × ca. 1 mm; tepals persistent on young fruit, covering the stigmas, outer pair ovate, 3–3.5 ×1–1.5 mm, inner pair oblanceolate, 2–3 × ca. 1 mm, delicately membranaceous, glabrous, with a conspicuous network of veins on both surfaces; styles three, free, 1–1.5 mm long, bifid, stigmatic area arranged in a spiral band; ovary green, ca. 6 mm long, glabrous and reticulate, spherical with three rib-like wings, placentation axile, one placentae per locule. *Fruits* pendulous, green, ca.10 × ca. 8 mm, with three wings, slightly unequal, the longer wing ca. 4 mm wide, shorter wings ca. 3 mm wide, glabrous, with a conspicuous network of veins.

Distribution and ecology.—*Begonia bernicei* is known from three gatherings collected in the understory of lowland moist forests in the lower Erebato river, in Bolívar state, Venezuela, all three coincidentally at an altitude of 360 m.

Because of its cymose inflorescence, ovary with three locules, female flowers with 4 perianth segments, male flowers with 2 perianth segments and one placenta per locule, *Begonia bernicei* belongs to the neotropical section *Doratometra* (Klotzsch) A. DC. (Doorenbos et al.1998). The annual plants asymmetric leaves, the few-flowered, one time dichotomous inflorescence, and the slightly unequal fruit wings place this new species close to *B. semiovata* Liebm. However, *B. bernicei* is distinguished by its leaves 7–14 × 4–8 cm (vs. 4.5–7 × 1–2 cm in *B. semiovata*), petiole 2–4 cm long (vs. 0.5–2 cm), inflorescence axillary and terminal, 6–8 cm long (vs. inflorescence axillary, 2–3 cm), tepals of the staminate flowers orbicular to reniform, 3 × 3 mm (vs. ovate to suborbicular, ca 2 × 2 mm), and tepals of the pistillate flowers 4 (vs. tepals of the pistillate flowers 5).

Etymology.—The epithet honors Bernice G. Schubert (1913–2000), noted authority on Dioscoreaceae, the genus *Desmodium* Desv. (Leguminosae-Papilionoideae), and particularly on Begoniaceae.

Paratypes: **VENEZUELA. Estado Bolívar:** Municipio Sucre, alrededores de Santa María de Erebato, 04'59'N; 64°49' O, 360 m, Feb 1989 (fl, fr), *E. Sanoja 2397, 2603* (PORT).

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MATELEA PAKARAIMENSIS (APOCYNACEAE: ASCLEPIADOIDEAE), A NEW SPECIES IN THE *MATELEA STENOPETALA* COMPLEX FROM GUYANA

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ABSTRACT

A new species of *Matelea* s.l. (Apocynaceae: Asclepiadoideae) is described from Guyana: **Matelea pakaraimensis.** The species belongs to the *Matelea stenopetala* species complex, but exhibits distinct differences in floral characters from previously known taxa, particularly in the color and vestiture of the corolla, as well as the structure of the gynostegium. An updated key to members of the complex is provided, including *M. grenandii*, *M. hildegardiana*, *M. quindecimlobata*, *M. stenopetala*, and *M. sucrensis*.

RESUMEN

Se describe una especie nueva de *Matelea* s.l. (Apocynaceae: Asclepiadoideae) de Guyana: **Matelea pakaraimensis.** La especie tiene afinidades con el complejo *Matelea stenopetala*, pero puede ser distinguida por diferencias en caracteres florales, específicamente el color y indumento de la corola, al igual que la estructura del gynostegio. Se provee una clave actualizada del complejo, que incluye *M. grenandii*, *M. hildegardiana*, *M. quindecimlobata*, *M. stenopetala*, y *M. sucrensis*.

Key Words: Apocynaceae, Gonolobinae, *Matelea*, gynostegium, South America

Matelea Aubl. (Apocynaceae: Asclepiadoideae: Gonolobinae) is a New World genus estimated to include 20–330 species, depending on its circumscription (Morillo 1997; Stevens 2001). More than 150 species have been named and at least eighty-four combinations made since the one hundred some combinations made by Woodson (1941). Because of Woodson's (1941) mass synonymization and the subsequent description of numerous new species, *Matelea* s.l. now represents a morphologically heterogeneous group (Morillo 1997; Stevens 2001; Krings & Saville 2007; Krings et al. 2008). Unfortunately, despite recent advances in our understanding of the Gonolobinae (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006; Krings et al. 2008), the circumscription of *Matelea* s.s. and numerous other lineages remains unresolved. Consequently, in the absence of improved generic level understanding of the Gonolobinae, it remains convenient to describe new species belonging to the subtribe into one of the three genera recognized by Woodson (1941): *Fisheria* DC. (dorsal anther appendages [Cd sensu Kunze 1995] vesicular), *Gonolobus* Michx. (dorsal anther appendages laminar), and *Matelea* s.l. (dorsal anther appendages absent). Ongoing study of the Gonolobinae in northern South America, as a component of the Smithsonian's Biological Diversity of the Guiana Shield Program, has now resulted in the discovery of an additional species of *Matelea* from northern South America.

The new species belongs to the *Matelea stenopetala* Sandwith complex, to which five species have been previously referred: *M. grenandii* Morillo, *M. hildegardiana* Morillo, *M. quindecimlobata* Farinaccio & W.D. Stevens, *M. stenopetala*, and *M. sucrensis* Morillo (Morillo 1980, 1988, 1991; Farinaccio & Stevens 2009). Among these, adaxially pubescent corolla lobes are found in the (1) new species described below (corolla purplish), (2) *M. hildegardiana* (corolla green or greenish-white), and, very rarely, in (3) *M. stenopetala* (see *Mori 24547*, US; corolla greenish-white to greenish-yellow). All other species in the complex—and usually *M. stenopetala* as well—exhibit adaxially glabrous corolla lobes. The recently described *M. quindecimlobata* is particularly interesting among these in bearing staminal corona lobes (Cs sensu Liede & Kunze 1993) trapezoidal in outline with the outer margins deeply irregularly 3–6-lobed-fimbriate and the lateral lobules broader than the central lobule (Farinaccio & Stevens 2009). *Matelea grenandii*, *M. stenopetala*, and *M. sucrensis*, in contrast, lack this character. They can be distinguished by the shape and size of the calyx and corolla lobes as noted in the key below.

Corona morphological terminology follows Liede and Kunze (1993) and Kunze (1995), although it is recognized that additional work may be needed to clarify issues of family-wide homology (see Endress & Bruyns 2000; Livshultz 2003). Shorthand abbreviations for corona morphology following Liede and Kunze (1993) and Kunze (1995) are as follows: Ca = annular corona of coralline derivation (faucal annulus); Cd = dorsal anther appendage; Ci = interstaminal corona; C(is) = fused interstaminal and stamina corona; Co = corpusculum; Cs = staminal corona.

KEY TO THE *MATELEA STENOPETALA* COMPLEX OF NORTHERN SOUTH AMERICA

1. Adaxial corolla lobe surface pubescent.
    2. Gynostegial corona distinctly elevated by a subtending 0.3–0.4 mm tall stipe, basal C(is) lobes thus not touching the corolla surface __________ **M. stenopetala**
    2. Gynostegial corona not elevated by a subtending stipe, basal C(is) lobes sitting on the corolla surface.
        3. Corolla lobes green or greenish-white with darker veins; Cs ridge rising vertically at more or less a right angle relative to its base, apex about the same distance from the gynostegial center as the base __________ **M. hildegardiana**
        3. Corolla lobes purplish; Cs ridge rising vertically at a distinctly acute angle relative to its base, apex distinctly more distant from the gynostegial center than the base __________ **M. pakaraimensis**
1. Adaxial corolla lobe surface glabrous.
    4. Cs lobes trapezoidal in outline, outer margins deeply and irregularly 3–6-lobed-fimbriate, lateral lobules broader than the central lobule __________ **M. quindecimlobata**
    4. Cs lobes various, but not lobed-fimbriate as above.
        5. Corolla lobes ovate, less than 1.5 times as long as wide, 3.3–4.1 × 2.5–3.0 mm __________ **M. sucrensis**
        5. Corolla lobes oblong, linear-lanceolate, or narrowly ovate-elliptic, 1.8–3 times as long as wide, 2.9–4.3 × 1.0–2.4 mm.
            6. Calyx lobes ovate, 1.35–1.4 × 1.0 mm; corolla lobes narrowly ovate-elliptic, 4.2–4.3 × 1.8–2.4 mm __________ **M. grenandii**
            6. Calyx lobes lanceolate or linear-lanceolate, 1.0–2.0 × 0.2–0.8 mm; corolla lobes oblong or linear-lanceolate, 2.9–3.6 × 1.0–1.5 mm __________ **M. stenopetala**

Matelea pakaraimensis Krings, sp. nov. (**Fig. 1**). Type: GUYANA. Potaro-Siparuni: Pakaraima Mountains, upper Ireng watershed, Sukabi River, 300 m below Andu Falls at Kukuinang Creek, 5°6'N 59°57'W, elev. 670 m, 20 Oct 1994 (fl), *P. Mutchnick 122 with T. Henkel and R. Williams* (holotype: US!).

Species nova *Mateleae* a *M. stenopetala* et affinibus lobis corolla purpureis in superficie adaxiali pubescentibus, stipite subtendenti coronam staminalem intrastaminalemque nullo, et corona staminali ascendenti sub angulo distincte acuto cum sua basi distinguenda.

Slender, woody vine. Stems glabrescent to somewhat pubescent, pubescence ubiquitous, not in lines, eglandular trichomes very sparse, retrorse when present, ca. 0. 4 mm long, glandular capitate trichomes sparse to moderately dense, spreading, ca. 0.1 mm long. Leaf blades narrowly elliptic to obovate, 8.2–13.8 × 2.8–5.4 cm, adaxial surface glabrous, midvein glabrous or pubescent, eglandular trichomes absent, glandular capitate trichomes spreading when present, ca. 0.1 mm long, abaxial surface glabrous, midvein glabrous, apices acuminate, bases cuneate, margins entire, colleters 4, lanceoloid, 0.25–0.5 mm long; petioles 12.0–28.6 mm long, moderately to densely pubescent, pubescence ubiquitous, eglandular trichomes rare, spreading when present, ca. 0.4 mm long, glandular capitate trichomes spreading, ca. 0.1 mm long. Inflorescence racemiform, peduncles to 8.4 mm long, moderately to densely pubescent, pubescence ubiquitous, eglandular trichomes rare, spreading when present, ca. 0.2 mm long, glandular capitate trichomes spreading, ca. 0.1 mm long; pedicels 8.5–9.3 mm long, moderately to densely pubescent, pubescence ubiquitous, eglandular trichomes rare, spreading when present, ca. 0.2 mm long, glandular capitate trichomes spreading, ca. 0.1 mm long. Calyx lobes lanceolate to lance-ovate, 2.0–2.5 × 1.0–1.5 mm, adaxial surface glabrous, abaxial surface moderately to densely pubescent, eglandular trichomes absent, glandular capitate trichomes spreading, ca. 0.1 mm tall, apices obtuse, margins entire; colleters 1 per sinus, lanceoloid, ca. 0.28 mm tall. Corolla purplish (fide collectoris), subcampanulate at base, tube ca. 1.0 × 1.2 mm, lobes imbricate in bud, linear-lanceolate to oblong, 4.2–4.5 × 1.5–1.8 mm, not ocellate, adaxial surface pubescent, eglandular trichomes spreading, ca. 0.08–0.1 mm long, glandular-capitate trichomes absent, abaxial surface moderately pubescent, eglandular

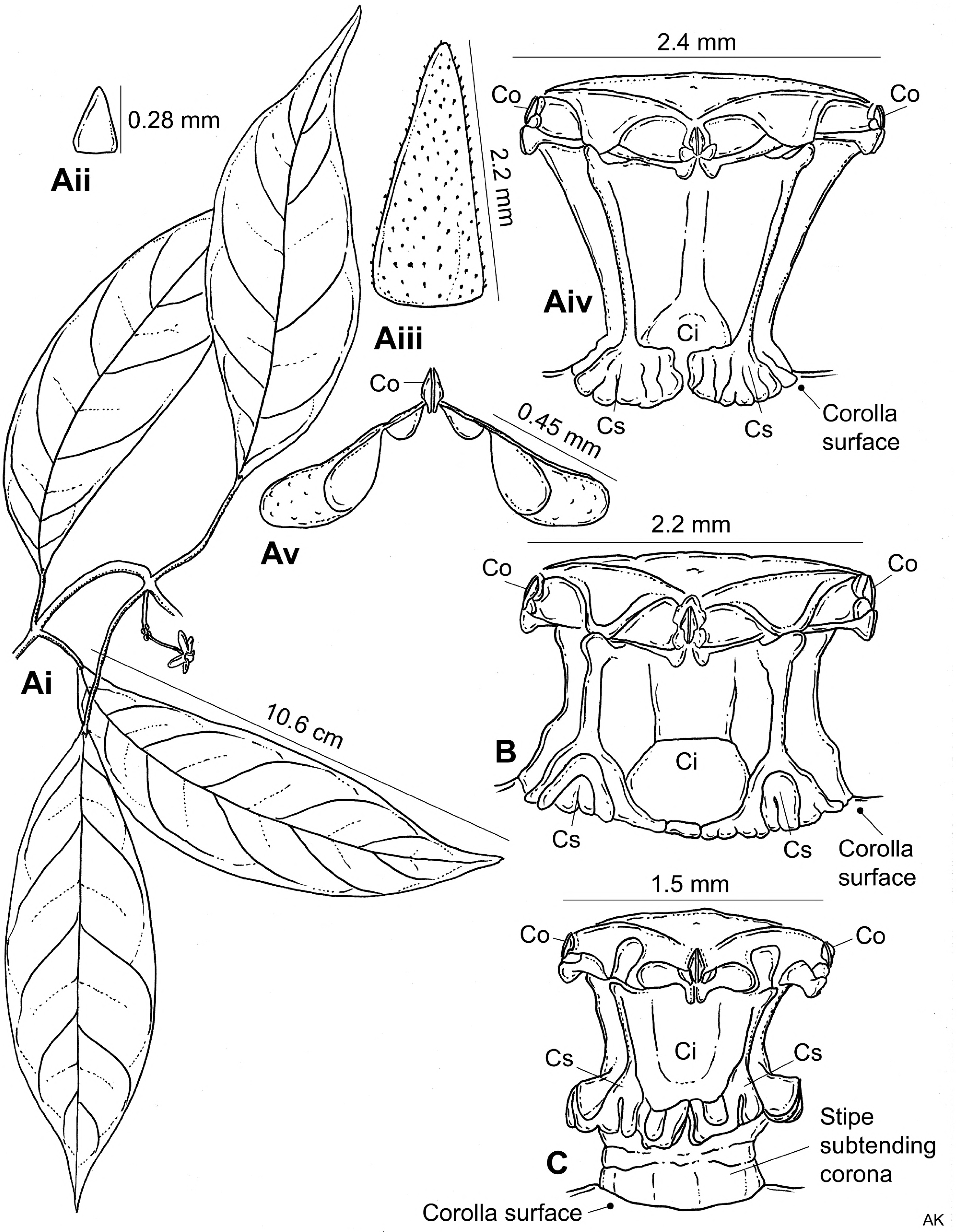

Fig. 1. Morphology of the three species in the *Matelea stenopetala* complex exhibiting corolla lobes adaxially pubescent (note that this character state is very rare in *M. stenopetala*): A, *M. pakaraimensis* (i, habit; ii, calycine colleter; iii, calyx lobe; iv, gynostegium; v, pollinarium; based on *Mutchnick 122* [holotype, US]); B, *M. hildegardiana* (gynostegium based on *Davidse 4903* [paratype, US]); C, *M. stenopetala* (gynostegium based on *Mori 24547* [US]). Ci = interstaminal corona; Co = corpusculum; Cs = staminal corona.

trichomes antrorse, ca. 0.15 mm long, glandular capitate trichomes spreading, ca. 0.03 mm long, apices obtuse, margins entire. Faucal annulus (corolline corona or Ca) absent. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, C(is) on the surface of the corolla lobes, not subtended by a stipe, Cs rising to meet the lower portion of the anther, rising segment at a distinctly acute angle relative to the base, apex

distinctly more distant from the gynostegial center than the base, base somewhat swollen, lobed, and slightly fimbriate, ca. 1.2 mm tall, ligule an apical ridge, not free, Ci unlobed, not ligulate. Style-head ca. 2.4 mm diam, stipe 1.2 mm tall, terminal style-head appendage absent. Pollinarium: corpuscula ca. 0.2 mm long, caudicles present, pollinia oblong, ca. 0.45 × 0.2 mm. Follicles unknown. Seeds unknown.

Notes.—Matelea pakaraimensis is currently known only from the type, which was collected in tall mesic forest on sandy soils. It is named after the mountain range in which it was found.

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A NEW COMBINATION BASED ON *MYRCIANTHES IRREGULARIS* (MYRTACEAE)—A NEW GENUS FOR ECUADOR

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ABSTRACT

Myrcianthes irregularis McVaugh, a rare and endemic species of Ecuador, is transferred to *Amomyrtella* Kausel. A key is provided for the two species of *Amomyrtella.*

Key Words: Myrtaceae, *Amomyrtella*, Rivero y Ustariz

RESUMEN

Myrcianthes irregularis McVaugh, una especie escasa y endémica de Ecuador, se translada a *Amomyrtella* Kausel. Se presenta una clave para las dos especies de *Amomyrtella.*

Myrcianthes irregularis, is a rare and endemic species of Ecuador that was until now known only from the type specimen. It was described by McVaugh in 1963, listed in the Catalogue of vascular plants of Ecuador (Jorgensen & León-Yanez 1999), and is considered a threaten species in the Ecuador Plants Red List (Valencia et al. 2000). McVaugh placed his new species in *Myrcianthes* based mainly on the characters of 4-merous flowers, dichasial inflorescence and small number of ovules. In her study of *Myrcianthes* Grifo (1992) realized that *M. irregularis* did not belong in that genus but was unable to place it with certainty in another. She did suggest that it was similar to *Psidium molle* Bertol. (=*P. guineense* Sw.) and it appears as a synonym of that species in the World Checklist of Myrtaceae (Govaerts et al. 2008). Seed characters are especially useful in placing species of American Myrtaceae into the proper genus (Landrum & Sharp 1989; Landrum & Kawasaki 1997). Fruits and seeds have only become available for this taxon since 1990 and matching these recent fruiting specimens with the type of *M. irregularis*, a specimen in bud and flower, has taken a while longer. We here transfer *M. irregularis* to *Amomyrtella*, a genus known until now to include a single species, *A. guili* (Spreg.) Kausel, from northeastern Argentina and southern Bolivia.

Amomyrtella, of the subtribe Myrtinae, is characterized by: 4-merous flowers; a subapical placenta with few ovules; a hard shiny seed coat with an operculum and a C-shaped inner cavity; and an embryo with the hypocotyl much longer than the cotyledons. We have not seen the embryo of *Myrcianthes irregularis*, but in all the other characters it matches *A. guili*. The only other genus that might be considered for *Myrcianthes irregularis* is *Pimenta* (another member of the Myrtinae), because of the similar species *P. pseudocaryophyllus* (Gomes) Landrum, especially var. *fulvescens* (DC.) Landrum. That species has a similar placentation and ovule number, 4-merous flowers, and the seeds are hard and lustrous and operculate. The seed cavity is more open, allowing for a coiled embryo (Landrum 1986, fig. 30G), and not C-shaped as it is in *Amomyrtella* and most other genera of hard seeded American Myrtinae.

Amomyrtella irregularis (McVaugh) Landrum & Morocho, comb. nov. (**Fig. 1**). *Myrcianthes irregularis* McVaugh, Fieldiana, Bot. 29:489. 1963. Type. ECUADOR. Loja: Bosque de "La Mira," Hda. La Hamaca, Catacocha, alt. 2400–2600 m, 17 Apr 1944, *Acosta-Solis 7923* (holotype: F, http://plants.jstor.org/specimen/f0092937f, = ASU photo).

Additional specimens examined. **ECUADOR. Loja:** Loja – La Toma, new road at "La Virgen," (3°57'S, 79°17'W), secondary forest and Machia vegetation, 2500 m, 22 Jul 1990 (fl, fr), *P. M. Jorgensen, C. Ulloa & M. Gavilanes 92016* (AAU, ASU, MO, QCA, QCNE); road Loja – Catamayo, montane cloud forest remnant (3°59'S, 79°16'W), 2580 m, 12 May 2007 (fr), *J. Hormeier, F. Werner, L. Chambers & K. Ledesma 2584* (ASU, SEL).

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Fig. 1. *Amomyrtella irregularis*. All from *P. M. Jorgensen, C. Ulloa & M. Gavilanes 92016*. A (at QCA), portion of herbarium specimen. B (at ASU), on left, an entire seed showing lustrous seed coat; on right, seed coat in section showing C-shape inner cavity. The operculum in the sectioned seed coat is in the lower right. C (at QCNE), hirsutulous inflorescence and young leaves.

Common name.—According to Acosta-Solis the common name is "mate-mate."

We contrast the two known species of *Amomyrtella* in the key below.

1. Leaves lanceolate, ovate, narrowly elliptic, or elliptic, 1.4–2.8 times as long as wide, obscurely puberulent to glabrous on lower surface; apex acute to acuminate, sometimes apiculate; base acute, acuminate, often unequal; peduncles glabrous to puberulent, uniflorous, usually borne in opposite pairs on short bracteate shoots ____ **A. guili**
1. Leaves suborbicular, elliptic or ovate, 0.7–1.4 times as long as wide, hirsutulous or pubescent on lower surface; apex usually rounded, less often acute, the tip occasionally apiculate; base rounded to cordate; peduncles densely hirsutulous, usually bearing a 3–7-flowered dichasium, the flowers sessile, subsessile, or the lateral flowers borne on pedicels up to 4 mm long ____ **A. irregularis**

Specimens of Rivero.—At P there are three sheets of *Amomyrtella irregularis* that seem to represent a single gathering. The labels all have written on them "M. Rivero, 1836, Pérou." There is no additional information. "Rivero" probably refers to Mariano Eduardo de Rivero y Ustariz, (1778–1857) an important Peruvian scientist of the 19th century. An account of his life can be found at http://en.wikipedia.org/wiki/Mariano_Eduardo_de_Rivero_y_Ustariz. He was in Peru in 1836 and may at that time have been the head of the National Museum of Natural History, Antiquities and History. He also worked as a director of the School of

Mines, as a diplomat and as a politician. His main interest was in geology but he is known to have had an interest in plants as well. Whether or not these specimens were collected by Rivero, and whether they were collected in Peru or Ecuador, is uncertain. They were annotated as *Psidium fulvum* McVaugh, by McVaugh himself in 1968, but on close examination clearly do not belong to that species. Collectors in Peru should be aware that *A. irregularis* may be encountered in that country someday.

Conservation status.—The two most recent collections of *Amomyrtella irregularis* were collected not far from Loja and only about 4 kms apart from each other. The exact locality of the type is unknown, but the town of Catacocha, mentioned on the label, is about 50 kms away. Thus, the three known collections probably fall within a circle of less than 3000 sq. km. Based on the criterion D-2 under vulnerable (VU) of the IUCN Redlist Categories (http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria) we suggest that *Myrcianthes irregularis* should be listed as VU as it is known from very few localities. These happen to be near the city of Loja where growth can be expected. Further studies may indicate that a classification of endangered (EN) would be more appropriate.

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BOOK REVIEWS

Jennifer Molnar (ed.). 2010. **The Atlas of Global Conservation: Changes, Challenges, and Opportunities to Make a Difference.** 2010 (ISBN 978-0-520-26256-0, hbk.). University of California Press, The Nature Conservancy, University of California Press, 2120 Berkeley Way, Berkeley, California 94704-1012, U.S.A. (**Orders:** California-Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, New Jersey 08618, U.S.A.; Toll-free 1-800-UC-BOOKS or 1-800-777-4726; Toll-free fax 1-800-999-1958; Customer service 1-609-883-1759; Email orders@cpfsinc.com). $49.95, 234 pp., color maps and graphics, 11¼" × 8¾".

This is an important and very timely book and should be read by everyone who purports to be a conservationist/environmentalist or who has any interest in the subject. The introductory essay by Paul Ehrlich alone is essential reading especially for those who question the reasons for preserving endangered species. Beyond these readerships, the book should also stand as an authoritative reference for the many aspects of conservation, of dwindling resources, of global threats, of plant and wildlife endangerment, and of human activity related to those topics.

Arranged in broad headings: habitats, covering each biome; the species and their importance in the ecosystem; the major changes in the world including population growth and climate change, and finally practical measures that man can take to alleviate if not always correct the problems. This is an atlas, and each topic has a world map that indicates the degree to which the areas are affected. For example, "Grasslands" shows the percentages of such areas by colored scale, from zero to 100%. The accompanying text explains the problems, historical and current, that may be of concern. The fifth part of the book is "Taking Action,' and the authors take into account the complexities of the subject. It is not just Americans helping to preserve tropical rainforests (and we must acknowledge how we in the United States have exploited our forests too, when it was deemed important for agriculture or for industry.) Protecting the earth must mean preservation of biodiversity, and that will involve national mandates and international cooperation, some of which will be in the form of strict laws and regulations, and necessarily individual action. It comes down to the fact, as one author of the book put it, that human well-being relies on functional ecosystems, and that ecosystems must have human management, to protect biodiversity while achieving societal goals.

One appendix has a map of each ecoregion and a list of the significant areas in that region. Technical notes and references for further reading are provided in a second appendix.

In addition to the editor, eight experts in their special fields have provided concise and cogent essays—on conservation and its "four threads": population, environment, economics, and culture.—*Joann Karges (TCU Library, Retired) and BRIT volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76107-3400, U.S.A.*

Andrea Wulf. 2011. **Founding Gardeners: The Revolutionary Generation, Nature, and the Shaping of the American Nation.** (ISBN 978-0-307-26990-4, hbk.). Alfred A. Knopf, 1745 Broadway, New York, New York 10019, U.S.A. (**Orders:** http://knopf.knopfdoubleday.com/; 212-782-9000). $30.00, 352 pp., b/w and color, 6¼" × 9¼".

A visit to Monticello, Thomas Jefferson's home in Virginia shows the deep interest our third president had in agriculture and gardening. Many of the founders of our country were landowners and farmers and were deeply involved in the development of plant cultivation. In addition, the vast new world was being explored and naturalists were collecting and propagating plant species that were not familiar to the Europeans who settled the country.

The accomplishments of founders in the historical context are well known, but Andrea Wulf has shined a light on the down-to-earth efforts of many of these figures in collecting and disseminating crops and ornamental plants that have become the mainstays of American gardens and farms.

In addition to Jefferson, the author details the contributions of John Bartram, Benjamin Franklin, John Adams, and George Washington among others. Plants were domesticated, seeds were traded, and gardens established by these founders even while they were otherwise occupied with the new country in North America.

This book is a great read for any of us with an interest in botany, agriculture, and American history. It points out some of the less well known challenges of establishing a thriving community and culture in the new land. The founders saw agriculture as the pathway to independence from Britain and they invested time, money, and attention to the plants that would build the future of the United States. The author has researched the subject thoroughly and includes maps and paintings of the estates of Washington, Jefferson, Madison, and Adams.

This book was reviewed in the New York Times Book Review May 8, 2011.—*Richard Lankow, PhD., Aspen Bioscience LLC, Fort Worth, Texas and BRIT volunteer, Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A.*

LECTOTYPIFICATION OF THOMAS NUTTALL'S NAMES APPLIED TO NORTH AMERICAN *POLYGALA* (POLYGALACEAE)

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ABSTRACT

Lectotypes for *Polygala alba* Nutt., *P. ambigua* Nutt., *P. attenuata* Nutt., *P. balduinii* Nutt., *P. boykinii* Nutt., *P. fastigiata* Nutt., *P. pubescens* Nutt., and *P. purpurea* Nutt. are newly designated. These names apply to North American taxa and were published by Thomas Nuttall in 1818 and 1834. Even though Nuttall's earlier collections are primarily deposited in the herbarium of the Academy of Natural Sciences, Philadelphia (PH), duplicates are also deposited at BM, CGE, LIV, and MANCH. Previous confusions on type designations are clarified.

Key Words: Baldwin, Boykin, herbarium BM, herbarium CGE, herbarium LIV, herbarium MANCH, herbarium PH, Lewis and Clark expedition, Nuttall, Pickering, *Polygala*, typification

RESUMEN

Se designan por primera vez los lectotipos de *Polygala alba* Nutt., *P. ambigua* Nutt., *P. attenuata* Nutt., *P. balduinii* Nutt., *P. boykinii* Nutt., *P. fastigiata* Nutt., *P. pubescens* Nutt., y *P. purpurea* Nutt. Estos nombres se aplican a taxa norteamericanos y fueron publicados por Thomas Nuttall en 1818 y en 1834. A pesar de que las primeras colecciones de Nuttall fueron depositadas principalmente en el herbario de la Academia de Ciencias Naturales de Filadelfia (PH), sus duplicados también se encuentran en BM, CGE, LIV, y MANCH. Se clarifican previas confusiones sobre la designación de los tipos.

INTRODUCTION

Since the founding of the Academy of Natural Sciences in Philadelphia in 1812, botanical collections of many North American species have been deposited at this institution (Freire-Fierro 2008). However, the type status of many has not been verified. Such is the case for many taxa described by Thomas Nuttall (1818, 1834), who used the Academy's herbarium (PH) as his home institution during the early stages of his career in the United States (Pennell 1936). In publications and on specimen labels, Nuttall generally added an asterisk before his new names for the plant species he described. Also, many of the PH Nuttall labels have the abbreviation "Nutt." in parenthesis. According to Stuckey (1966), this abbreviation had been added later by Charles Pickering (1805–1878) (Fig. 1). Following standard practice, we could have chosen Nuttall specimens at PH as the holotypes. We did not to do that, however, because Nuttall generally studied more than one specimen per species, and he was not consistent in the use of the asterisk (Stuckey 1966). In several instances, he did not provide much detail about the localities. Additionally, material used by him for the description of new taxa is also deposited at several herbaria (e.g., BM, CGE, LIV, and MANCH). These facts, combined with the scarcity of current published literature on North American Polygalaceae (Wendt 1979) and the familiarity of AFF with Polygalaceae, motivated the initiation of this project.

This paper presents results obtained from a study on the types of North American *Polygala* (Polygalaceae) described by Thomas Nuttall (1818, 1834) and deposited at the Academy of Natural Sciences, Philadelphia (PH). This genus has 1,554 species described, and less than 40% of these have been taxonomically/nomenclaturally assessed (The Plant List 2011). So, the current total estimate of 300–350 species (Eriksen & Persson 2006) is very likely an underestimate (R. Abbott, pers. comm., 2011). Although there are various floristic and taxonomic revisions for the genus that include taxa from the United States (Chodat 1893; Blake 1916, 1924; Smith & Ward 1976; Wendt 1979; Gleason & Cronquist 1991 and Bernardi 2000), these do

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Fig. 1. Handwritings of Thomas Nuttall (in pencil) with Charles Pickering's abbreviation "Nutt." (in ink).

not include a complete nomenclatural type status for all the taxa. However, and according to the ongoing treatment of Polygalaceae for Flora of North America north of Mexico, Abbot considers that there are 53 spp. of *Polygala* s.l. for the region (R. Abbott, pers. comm., 2011).

PH holds types for 53 of New World names of *Polygala*, including the following species described by Nuttall in 1818: *Polygala alba*, *P. ambigua*, *P. attenuata*, *P. balduinii*, *P. brevifolia*, *P. fastigiata*, *P. pubescens,* and *P. purpurea*, and in 1834: *P. boykinii*. Type verification followed Article 9 of the ICBN (McNeill et al. 2006) and was carried out by conventional methodologies. Online resources such as IPNI (2011), Tropicos (2011), The Plant List (2011), and TL-2 Online (Stafleu & Cowan 1983; Stafleu & Mennega 1995) were also consulted.

TYPIFICATION

Polygala alba Nutt., Gen. N. Amer. Pl. 2:87. 1818. (**Fig. 2**). Type: U.S.A. "On the plains of the Missouri:" Mar 1811, *Nuttall & Bradbury s.n.* (lectotype, designated here: PH 1049944 p.p. [rightmost specimen]!; isolectotype: BM, R. Kennedy, pers. comm. 2008).

Polygala senega L. var *tenuifolia* Pursh, Fl. Amer. Sept. 2:750. 1814 [Dec 1813] [published as *Polygala seneca* γ *tenuifolia*]. Type: U.S.A.: "On the Missouri," 10 Aug 1806, *M. Lewis s.n.* (lectotype, designated by Cutright 1969: 415: PH-LC 173!). Syntype: U.S.A. "Louisiana" [Territory]: 1811, *M. Bradbury s.n.* (LIV digital image!, PH 1021754!).

For verification, Nuttall's original description was positively matched with his handwriting on the PH label describing "Missouri" as the locality. According to Ewan's (1971) chronology of Nuttall's travels in North America, Nuttall (and collector Bradbury) "set out together on foot for St. Charles on the Missouri, on the first lap of Astorian Expedition to the Mandan Villages" in March, 1811. Although there are no additional Nuttall duplicates of *P. alba*, it is very likely that the Bradbury specimen deposited at LIV, besides being the syntype of *Polygala senega* var. *tenuifolia*, is also a topotype of *Polygala alba*. Pursh, in the *Addenda et Corrigenda* section of his *Fl. Amer. Sept.* (1814: 750), cited a Bradbury and a Lewis collection under this name: "*Polygala senega* [published as Seneca] adde var. γ *tenuifolia*." Four years later, Nuttall (1818) stated that these plants were much more than a variety, thus designating them as a new species.

In the description of his new variety, Pursh wrote "foliis linearibus, spicis confertifloris. On the Missouri. Lewis and Bradbury v.s." In the protologue, Pursh states that he saw two Missouri specimens [v.s.], one collected by Meriwether Lewis during the Lewis and Clark Expedition of 1804–06, and the second collected by Bradbury, likely on the same trip with Nuttall in March of 1811.

Since PH contains almost the entire Lewis and Clark plant collection, we were able to locate the specific specimen cited by Pursh, which had been designated as lectotype by Cutright (1969). Although without any associated publication, M.C. Johnston in 1958 annotated the PH sheet as "Type" of the variety. Cutright (1969) effectively lectotypified it.

Polygala ambigua Nutt., Gen. N. Amer. Pl. 2:89. 1818. (**Fig. 3**).

Polygala verticillata L. var. *ambigua* (Nutt.) Alph.Wood, Class-book Bot. (ed. 1861): 296. 1861. Type: U.S.A. New Jersey: "In New Jersey and Virginia," *Nuttall s.n.* (lectotype, designated here: PH 1049943 p.p. [rightmost specimen]!; isolectotypes: BM, R. Kennedy, pers. comm. 2008; CGE digital image!).

The lectotype specimen has Nuttall's handwriting including his signature asterisk and it gives the locality as "N. Jersey." William T. Gillis (1933–1979) annotated this specimen as lectotype on 20 June 1975. However, no publication by Gillis regarding this lectotypification has been located. A second collection of the species made by Nuttall is also known from "Philadelphia" (*Nuttall s.n.,* K p.p. digital image!, MANCH digital images [2]!), and Nuttall annotated those specimens as *P. ambigua* at some point. Nevertheless, the protologue clearly states the distribution to be New Jersey and Virginia, and so this collection should not be considered type material.

Nuttall's name when used at the varietal rank was up until recently cited as *Polygala verticillata* L. var. *ambigua* (Nutt.) Britton [Trans. New York Acad. Sci. 9(2):9. 1889] in the various online databases (IPNI 2009 and Tropicos 2009). However, this combination was validly published decades earlier by Alphonso Wood in his Class-book of Botany (Wood 1861). This "class-book" went through numerous editions. In earlier editions, Wood (1846, 1850), recognizes *P. ambigua* Nutt. as a distinct species. However in the 1861 edition,

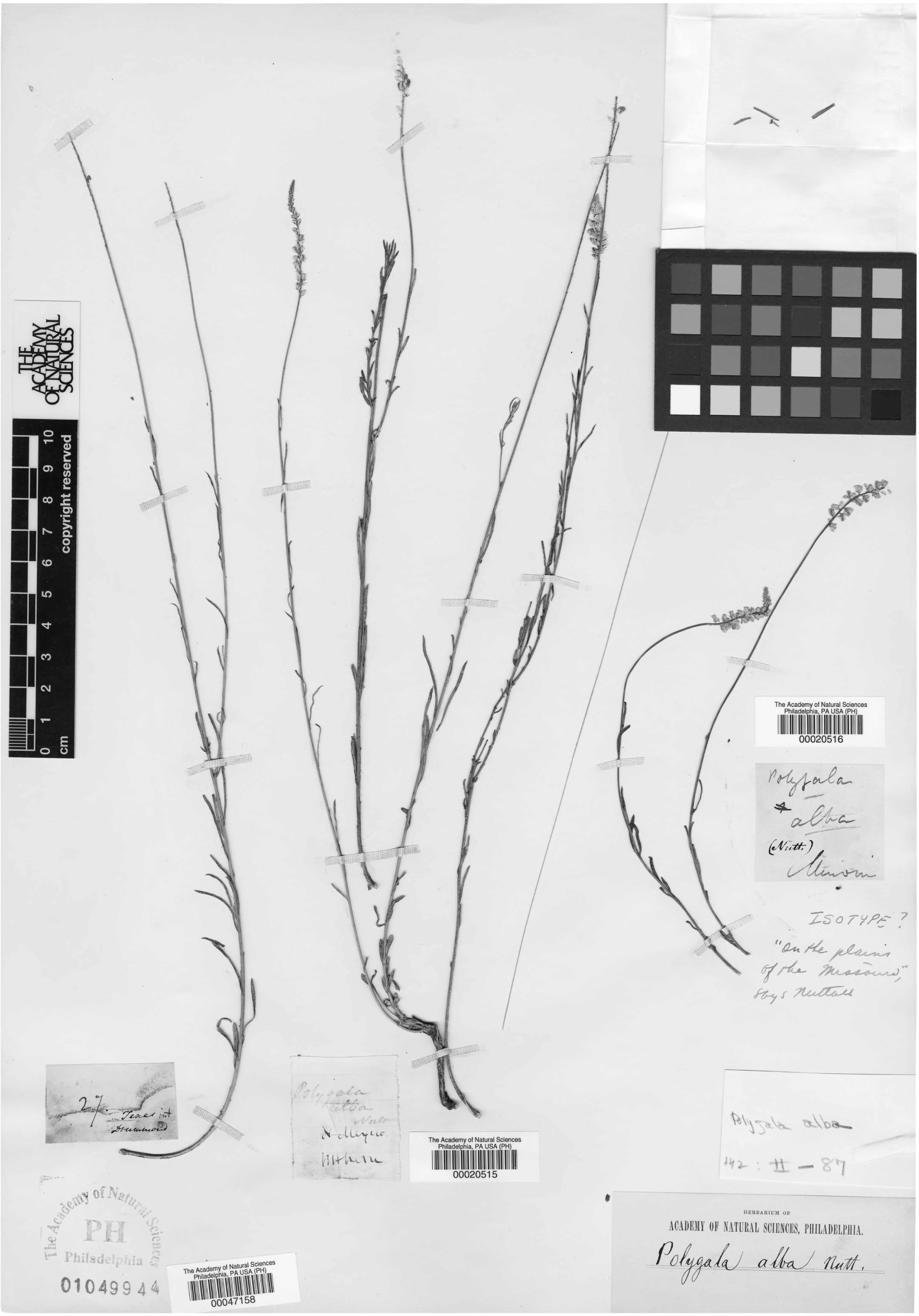

Fig. 2. Lectotype of *Polygala alba* Nutt. (PH 1049944 p.p. (rightmost specimen), barcode number 47158)

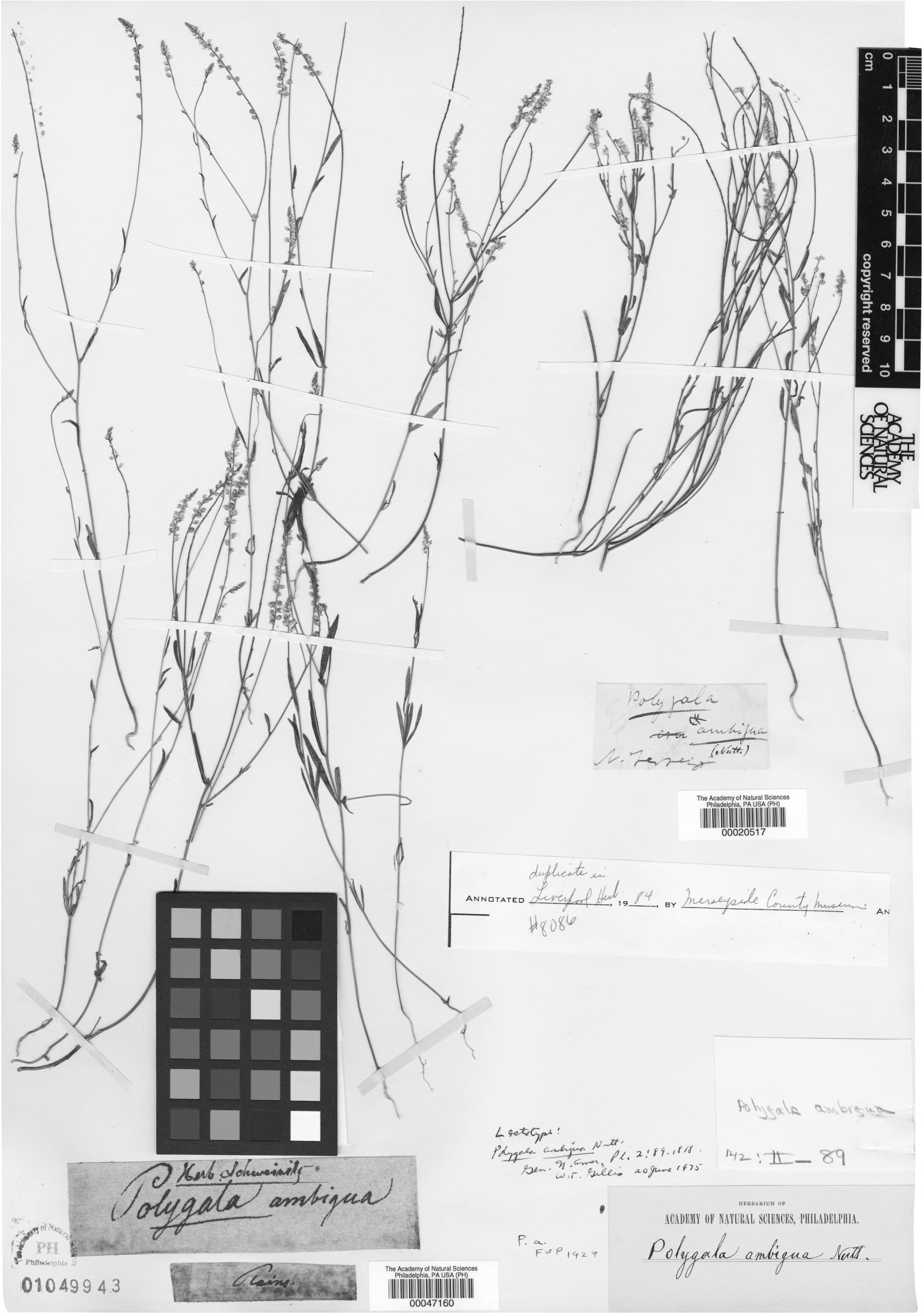

Fig. 3. Lectotype of *Polygala ambigua* Nutt. (PH 1049943 p.p. (rightmost specimen), barcode number 20517)

P. ambigua disappears as a species and the variety *P. verticillata* var. *ambigua* appears. Although Wood does not cite Nuttall's species *per se* with the new varietal name, it is absolutely clear from the context, description, and previous editions that he is referring to the same taxon that he previously treated as *P. ambigua* Nutt. Because Wood gives a full description of the variety, article 33.3 of the Vienna Code applies and this is considered a valid new combination based on the Nuttall basionym.

Polygala attenuata Nutt., Gen. N. Amer. Pl. 2:90. 1818. (**Fig. 4**). Type: U.S.A. Georgia: *Nuttall s.n.* (lectotype, designated here: PH 1049951 p.p. [leftmost specimen]!). Syntype: U.S.A. Georgia: *Baldwin s.n.* (PH 1049951 p.p.!).

Polygala praealta W. Baldwin ex Nutt. nom. nud.

At PH, there are four individual specimens belonging to the same species on the same herbarium sheet; we will discuss them from left to right (Fig. 4). With the first (leftmost) specimen, there is a Nuttall label with his characteristic asterisk and handwriting, "Polygala attenuata Georgia." The same label has also this text written: "(Nutt.) P. corymbosa Elliot," with darker ink. The locality mentioned is congruent with that from the protologue, which described the species' distribution "from North Carolina to Florida," and the plant matches the description given by Nuttall. This clearly is the best specimen to designate as lectotype.

The second specimen does not have Nuttall's handwritten label, but was collected in Georgia. The remaining two specimens are from the Schweinitz Herbarium. The first specimen from the Schweinitz Herbarium has the label '*Polygala praealta*', a name used by Baldwin but never published. Nuttall wrote that Baldwin called it *P. praealta* because of its height (2 to 3 feet tall), but because several species of *Polygala* are of similar height, Nuttall thought that the name was not distinctive. He thus renamed the species as *P. attenuata* because of the attenuate and tapered stem. Because of common practice of collecting duplicates, it is not farfetched to assume the lectotype is a duplicate of Baldwin's *P. praealta* and the specimen labeled similarly from the Schweinitz Herbarium was Baldwin's own specimen. The second specimen from the Schweinitz collection has the handwritten label "Herb. Schweinitz, Polygala, ad prima georgiana. N." but gives neither collector nor number. This specimen is morphologically similar to *P. attenuata* and it is very likely that "N." stands for Nuttall. If so, this specimen could be a duplicate of the lectotype.

Polygala attenuata Nutt. is currently considered a taxonomic synonym of *P. cymosa*, published in 1788 by Walter in his treatment *Flora Caroliniana* (Smith & Ward 1976).

Polygala balduinii [as *balduini*] Nutt., Gen. N. Amer. Pl. 2:90. 1818. (**Fig. 5**). Type: U.S.A. Florida: "Near St. Mary's in Florida," *Baldwin s.n.* (lectotype, designated here: PH 1049950 p.p. [leftmost specimen]!; probable isolectotype: BM, R. Kennedy, pers. comm. 2008).

The sheet PH 1049950 in the collection at PH clearly represents Nuttall's type. Morphologically it matches the description of *P. balduinii* in the protologue, its label is written in Nuttall's handwriting, it contains his signature asterisk detailing a new species, and the locality written "St. Mary's" exactly matches the protologue. Nuttall also mentioned that he received a specimen from "Dr. Baldwyn" under the name *P. polycephala*—the label gives 'Dr. B' as the collector, affirming the lectotype designation herein made. A second sheet (PH 1049949) of this species is part of the Schweinitz collection and is also labeled *P. polycephala,* but with the annotation "Polygala polycephala Baldwini Nut." in Schweinitz' handwriting. Schweinitz' label gives "LeConte" as the collector and "Georg.[ia]" as the locality—neither of which match Nuttall's specimen nor the protologue. Thus, this specimen should not be considered type material, given that the protologue specifically describes St. Mary's, Florida, as the distribution.

Polygala boykinii [as *boykini*] Nutt., J. Acad. Nat. Sci. Philadelphia 7(1):86. 1834. (**Fig. 6**). Type: U.S.A. Georgia: "In Georgia and Florida," *Boykin s.n.* (lectotype, designated here: PH 1049947!; isolectotypes: BM, R. Kennedy, pers. comm. 2008, PH 1049948!).

The PH type collection holds two specimens collected by Boykin. The first (PH 1049947) has a Nuttall label with the name "Boykinii" and the aforementioned asterisk. According to the protologue, Nuttall received a specimen from Boykin. We consider the second specimen (PH 1049948) to be Boykin's duplicate of the

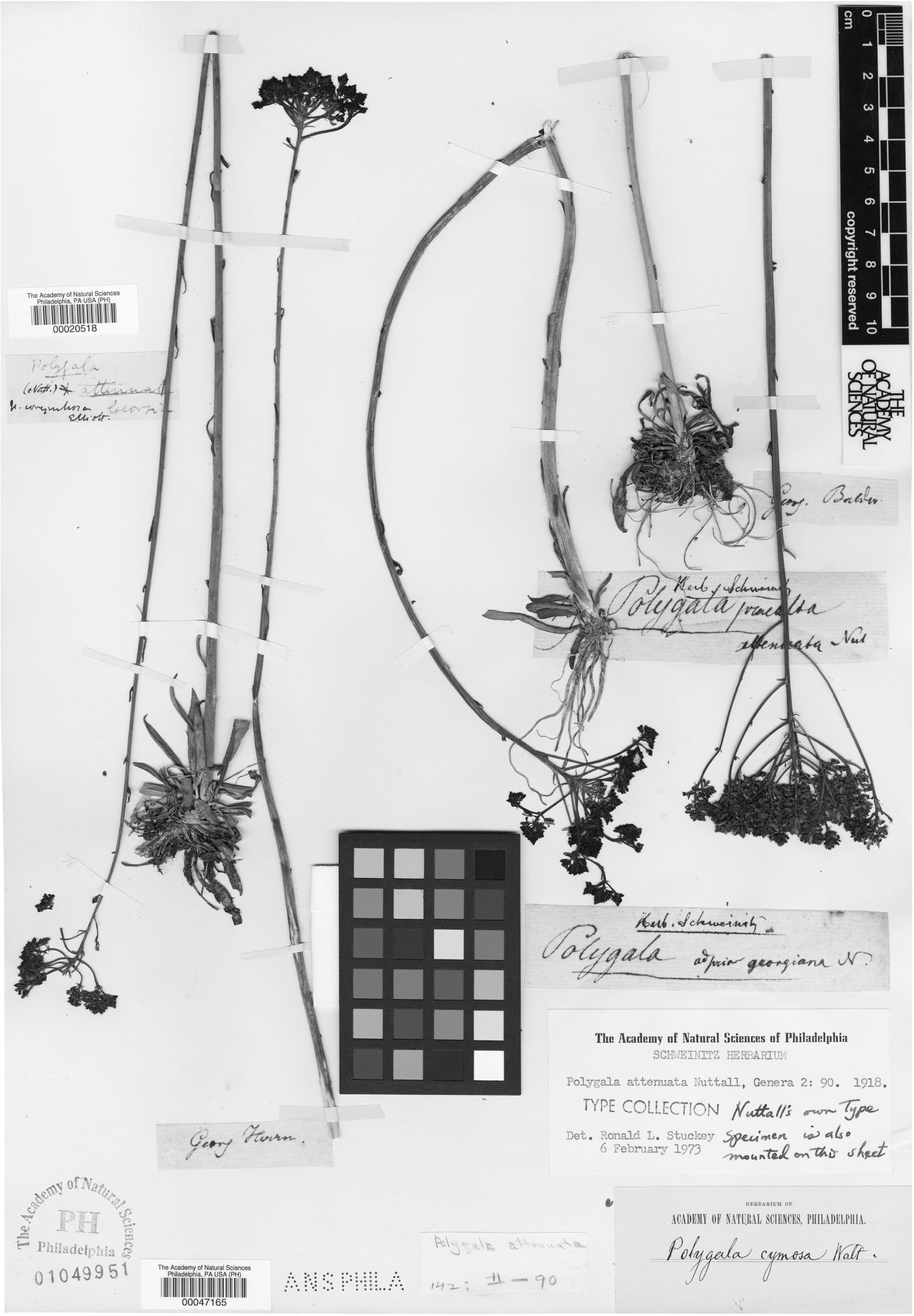

Fig. 4. Lectotype of *Polygala attenuata* Nutt. (PH 1049951 p.p. (leftmost specimen), barcode number 20518)

Fig. 5. Lectotype of *Polygala balduinii* Nutt. (PH 1049950 p.p. (leftmost specimen), barcode number 20519)

Fig. 6. Lectotype of *Polygala boykinii* Nutt. (PH 1049947, barcode number 47170)

same collection, because the localities are similar and because Nuttall appears to have opined on a duplicate of that specimen: the label contains a stamp "S. Boykin, (Ga.)" and a note that reads "Polygala, Mr. Nuttall says not *P. cruciata* what species then?" in a handwriting very likely to be Boykin's. This herbarium sheet also has attached to it a complete description of Nuttall's *P. boykini* in the same handwriting as the label. It is thus very likely that Boykin collected at least two specimens from the same plant, sent one to Nuttall for study, leading to Nuttall describing the species as new, and dedicating the name to Boykin. Nuttall's label is in his own handwriting, containing his signature asterisk, with two other, crossed out, specific epithets – firstly "Cruciata?" and then "senegoides." This latter specific epithet is also written on the BM specimen (R. Kennedy, pers. comm. 2008). While the protologue (Nuttall 1834) mentions the species' similarity to *P. bicolor* Kunth, and while the BM specimen also has the determination "P. bicolor" (R. Kennedy, pers. comm. 2008), the PH specimen does not include this information. Still, the PH specimen is certainly the one Nuttall received from Boykin, because of the handwritten "Cruciata?" on the label, which the BM specimen does not have. Also, Nuttall's specimen matches the protologue perfectly.

Although there is a lectotypification annotation made by W.T. Gillis on 20 June 1975 on PH 1049947 (as occurred for *P. ambigua*), a publication with his designation has not been located.

Polygala brevifolia Nutt., Gen. N. Amer. Pl. 2:89. 1818. Type: U.S.A. New Jersey: "New Jersey, also in Ohio," *Nuttall s.n.* (lectotype, effectively designated by Wheelock 1891: 119: PH 1049945!; isolectotype: BM, R. Kennedy, pers. comm. 2008).

The label of the lectotype has Nuttall's handwriting, his signature asterisk, and the locality ("N. Jersey") matching the protologue. The specimen also matches Nuttall's original description. Since there is no doubt that this specimen was the one studied by Nuttall, and Wheelock cited Nuttall's New Jersey specimen at PH as the "type," his lectotypification is followed.

Blake (1924) listed *P. brevifolia* as occurring only on the Coastal Plain, and Stuckey (1966) mentioned that the species is unknown from Ohio, even though Nuttall's protologue gives the distribution as "New Jersey, also in Ohio."

Polygala fastigiata Nutt., Gen. N. Amer. Pl. 2:89. 1818. (**Fig. 7**). Type: U.S.A. New Jersey: "In New Jersey, &c. v.v." *Nuttall s.n.* (lectotype, designated here: BM p.p. digital image (rightmost specimen)!; isolectotype: K digital image (4th specimen from the left)! Syntypes: U.S.A. New Jersey: "N. Ceasar." *I. Cleaver s.n.* (Muhlenberg collection p.p., PH 1092552 p.p. (second specimen from the left!); U.S.A. "Delaware:" *Nuttall s.n.* BM p.p. digital image (leftmost specimen)!.

In the protologue, Nuttall writes: "HAB. In New Jersey, &c. *v. v.* Nearly allied to *cruciata*, more remotely to *setacea*, with which it is confounded in Muhlenberg's Herbarium. *v. s.*"

Since no Nuttall specimen for this species is available at PH, we have chosen the BM specimen as the lectotype because it has Nuttall's handwriting and because it was collected in New Jersey [as "Nova Caesarian"].

Because Nuttall mentioned the "&tc" after "New Jersey" in the protologue, it is likely that he used the specimen from Delaware as well. We consider, therefore, his Delaware collection as the syntype.

The Muhlenberg sheet with a handwritten label "*Polygala cruciata* 940" has four specimens. The second specimen from the left has another label with the following Nuttall text handwritten: "Polyg. N. Caes. Cleaver; virid.?, vel tenella Baldwin; P. sanguinea? Lin. T.N." "N. Caes." stands for Nova Caesarea, the Latin name used for New Jersey (A.E. Schuyer, pers. comm. 2011). Additionally, and according to Mears (1978), the Philadelphia physician Isaac Cleaver "sent plants of New Jersey and other places to Muhlenberg in 1814." We consider this New Jersey specimen as a syntype, because it matches with the protologue, and it was studied and cited by Nuttall. The specimen at K is clearly a duplicate of the lectotype because the Nuttall label reads "Polygala fatigiata N. Gen. Am. N. Ceasarian." The Muhlenberg specimen of *Polygala setacea* (PH 1092555) does not correspond to the description of *P. fastigiata*, nor does it match with the lectotype and syntype.

Although a Nuttall specimen at CGE is morphologically similar to the ones at BM, K, and PH, it is not possible to know whether it was collected in Delaware or in New Jersey. If it can be shown to have been collected in New Jersey, then it should be considered a duplicate of the lectotype.

FIG. 7. Lectotype of *Polygala fastigiata* (BM p.p. rightmost specimens, barcode number 939164)

Fig. 8. Lectotype of *Polygala pubescens* Nutt. (PH 1072615 p.p. (leftmost specimen), barcode number 20567)

Fig. 9. Lectotype of *Polygala purpurea* Nutt. (K p.p. (leftmost specimen), barcode number 555052)

Polygala fastigiata, though described by Nuttall as closely related to *P. cruciata* L., was later synonymized under *P. mariana* Mill. (Blake 1924).

Polygala pubescens Nutt., Gen. N. Amer. Pl. 2:87. 1818. nom. illeg., later homonym non *P. pubescens* Mart. (1815). (**Fig. 8**). Type: U.S.A. Georgia: "Around Savannah in Georgia, &c," *Nuttall s.n.* (lectotype, designated here: PH 1072615 p.p. [leftmost specimen]!).

For the locality, Nuttall mentions in the protologue: "HAB. Around Savannah in Georgia, &c." So, it is likely that he collected it himself in Savannah (GA) while visiting Baldwin in the fall of 1815 (Ewan 1971). While the label allows for little identification, it does contain Nuttall's asterisk before the word "pubescens." Blake (1924) considered *Polygala pubescens* Nutt. a synonym of *P. grandiflora* Walt.

Polygala purpurea Nutt., Gen. N. Amer. Pl. 2:88. 1818, *nom. illeg.*, later homonym non *P. purpurea* Ait. f. Hortus Kew. (W.T. Aiton), ed. 2, 4:244. 1812. (**Fig. 9**). Type: U.S.A. New Jersey: "Common throughout North America," *Nuttall s.n.* (lectotype, designated here: K p.p. digital image [leftmost specimen]!; isolectotypes: CGE digital image!; LIV digital image!; PH 1072616 p.p.!).

When describing *Polygala purpurea*, Nuttall acknowledged that his specimen along with those described by Michaux and Pursh under *P. sanguinea* L. corresponded to a species distinct from the latter. From his description, it is evident that he also studied the Pursh material deposited at K, and also the one at PH (mounted on the same sheet with specimens identified as *Polygala sanguinea*). Although the PH specimen containing Nuttall's label ordinarily would have been designated as the lectotype, we chose the sheet at K because the sheet at PH has four labels and eight specimens that have been intermingled sometime in the past during the mounting process. Regarding the type locality, despite the fact that the protologue does not mention a particular location, the label at PH reads "Camden" (New Jersey) and the label at K reads "New Jersey."

According to Art. 64 from the *Code* (McNeill et al. 2006), the name *Polygala purpurea* Nutt. is considered illegitimate, because of the publication of an earlier homonym (*P. purpurea* Ait.f.) published in 1812 and based on another North American collection that had been introduced to Europe in 1791 (Aiton 1812). No new name is assigned to *P. purpurea* Nutt. because it was considered a synonym of *P. viridescens* L. (Blake 1924). Currently, the name *Polygala viridescens* L. is considered a synonym of *Polygala sanguinea* L. (Fernald 1950).

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NOTES ON THE DISINTEGRATION OF *POLYGALA* (POLYGALACEAE), WITH FOUR NEW GENERA FOR THE FLORA OF NORTH AMERICA

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ABSTRACT

Polygala (Polygalaceae) is polyphyletic as traditionally circumscribed, obfuscating our understanding of the species, their relationships, morphology, ecology, and biogeography. Based on phylogenetic data, I propose the recognition of the monophyletic groups **Asemeia** Raf., **Hebecarpa** (Chodat) J.R. Abbott, stat. nov., **Polygaloides** Haller, and **Rhinotropis** (S.F. Blake) J.R. Abbott, stat. nov. as genera. The remaining North American species are maintained within a more restricted and monophyletic delimitation of *Polygala*. These genera are all morphologically diagnosable, and all are traditionally recognized as infrageneric taxa of *Polygala*.

Key Words: *Asemeia*, *Hebecarpa*, new genera, North America, phylogeny, *Polygala*, Polygalaceae, *Polygaloides*, *Rhinotropis*

RESUMO

Polygala (Polygalaceae) na sua delimitação mais tradicional é polifilético, ofuscando nosso entendimento das espécies, suas relações filogenéticas, morfologia, ecologia e biogeografia. Baseado em dados filogenéticos, eu proponho o reconhecimento dos grupos monofiléticos **Asemeia** Raf., **Hebecarpa** (Chodat) J.R. Abbott, stat nov., **Polygaloides** Haller e **Rhinotropis** (S.F. Blake) J.R. Abbott, stat. nov. como gêneros. O restante das espécies Norte Americanas são mantidas em uma delimitação mais restrita e monofilética de *Polygala*. Estes gêneros são todos morfologicamente diagnosticáveis e eram tradicionalmente taxa infragenéricos de *Polygala*.

Palabras Clave: America do Norte, *Asemeia*, filogenia, *Hebecarpa*, novos gêneros, *Polygala*, Polygalaceae, *Polygaloides*, *Rhinotropis*

INTRODUCTION

Polygalaceae Hoffmanns. and Link of North America north of Mexico [hereafter referred to as North America] consist of one species of *Monnina* Ruiz and Pav. s.l., ca. 52 native species of traditional *Polygala* L., and four reportedly naturalized species of *Polygala* (only one of which, *P. vulgaris* L., appears to be truly naturalized). A morphologically diverse assemblage of herbs and shrubs, they are most speciose in the southern United States and occur in a wide range of habitats, from wetlands to woodlands or deserts, mirroring the global diversity and range of *Polygala*, which, as traditionally circumscribed, includes everything from annual herbs to lianas and trees, occurring from sea-level to high montane regions. Eriksen and Persson (2007) provided a comprehensive description of the family, as well as a discussion in which they pointed out that there are discrepancies between published phylogenetic analyses and that there is a lack of clarity with respect to relationships within the tribe *Polygaleae* Chodat. Nonetheless, all phylogenetic analyses have indicated that traditional *Polygala* s.l. is a polyphyletic assemblage (Eriksen 1993a; Persson 2001; Forest et al. 2007), i.e., that several groups of species are more closely related to other genera than they are to other *Polygala* species.

Traditionally, nearly anything with a falsely papilionoid flower (two petals forming a 'standard,' one conduplicate petal forming a 'keel,' and two petaloid lateral sepals forming 'wings') and with a bilocular capsule has been left in *Polygala*, while groups with conspicuous specialized features, primarily modified fruits, have been segregated as other genera. Globally, many additional infrageneric groups have been named, based on vegetative and reproductive differences, but there has been neither consensus on which groups to recognize nor agreement as to which rank is appropriate. There have been numerous regional floristic treatments, sometimes even of a monographic nature, which have suggested various morphological features for taxonomic use (e.g., Blake 1916, 1924; Marques 1979; Meijden 1988; Paiva 1998; Bernardi 2000), but not

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since Chodat's century-old work (1893, 1896) has there been a global treatment of the genus *Polygala*. Thus, there is no clear or reasonably comprehensive phylogenetic framework for assessing the level of universality for putative synapomorphies.

As a result, attempts to stress any morphological feature (or suite of features) as more important than any other for taxonomic purposes run the risk of being arbitrary or incomplete in focus. In the analyses of Eriksen (1993a), Persson (2001), and Forest et al. (2007), several of the traditional subgroups within *Polygala* have been shown to be non-monophyletic (or, if monophyletic, to make other groups non-monophyletic), while some subgroups have been supported as monophyletic and many smaller groups have simply not been adequately addressed. The two most complete phylogenetic analyses of Polygalaceae, both using only plastid sequence data, included 25 species of *Polygala* s.l. (Persson 2001), six of which occur natively in North America (a 7th, *P. vulgaris* L., is sparingly naturalized and an 8th, *P. violacea* Aubl. emend Marques, is part of a widespread complex that may include the North American *P. grandiflora* Walter), and 49 species of *Polygala* s.l. (Forest et al. 2007), seven of which occur in North America. It is clear that some of the North American species are more closely related to other genera than they are to each other, but a robust global phylogenetic context for assessing morphology and for generic circumscription has been lacking.

Forty-five species of North American Polygalaceae (a six-fold increase over the most complete published study), representing 80% of the ca. 53 native species and all of the traditional subgenera, sections, and series in North America north of Mexico, along with 90 extra-limital *Polygala* taxa and 44 members of other genera (including two legumes as the outgroup), were phylogenetically analyzed using nrITS and the plastid *trnL* intron and adjacent spacer *trnL-F* (2778 total aligned characters). Those analyses were important in shaping my taxonomic conclusions with respect to the Flora of North America treatment, and they will be discussed in a forthcoming publication. As per the requirement for new names to have been published prior to their use in the Flora of North America project, I present here a discussion of the morphologically diagnosable groups that I will be recognizing as genera of Polygalaceae in North America.

RESULTS

In all analyses, the tribe Polygaleae was resolved as monophyletic, and in no analyses were all species traditionally recognized as *Polygala* recovered as a monophyletic group (Fig. 1). Although the exact relationships between some of the clades within the Polygaleae were not consistently recovered, the following clades were consistently supported across all, or nearly all, analyses (taxa traditionally included within *Polygala* s.l. are indicated with an asterisk): *Acanthocladus* Klotzsch ex Hassk.*, *Asemeia* Raf.*, *Badiera* DC.*, *Bredemeyera* Willd. s.str., *Comesperma* Labill., *Hebecarpa* (Chodat) J.R. Abbott, stat. nov.*, *Heterosamara* Kuntze*, *Polygala* subgen. *Ligustrina* (Chodat) Paiva*, *Monnina* Ruiz and Pav., *Muraltia* DC., *Phlebotaenia* Griseb.*, *Polygala* L. s.str. (with an Old World subclade and a New World subclade), *Polygaloides* Haller*, *Rhinotropis* (S.F. Blake) J.R. Abbott, stat. nov.*, *Salomonia* Lour., and *Securidaca* L. In the few analyses where one of these clades was not recovered, it was a result of a lack of resolution and not from a well-supported conflicting topology. Although the addition of more taxa altered some supported relationships, the overall topology of most clades from the 56 taxa analysis is robust to the addition of taxa across the combined nuclear and plastid analyses, with robust support for the distinctiveness of the clades recognized or proposed herein as genera, as well as for several of the subclades within *Polygala* s.str.

GENERAL DISCUSSION

A representative example of historical attempts to reclassify the North American species of *Polygala* is provided by Small (1933), who recognized *Asemeia* Raf. (for *P. grandiflora* Walter and some N hemisphere allies no longer recognized as separate species), *Galypola* Nieuwland (for *P. incarnata* L.), *Pilostaxis* Raf. (for a few species in an endemic southeastern U.S. group also recognized as *Polygala* ser. *Decurrentes* Chodat), and *Trichlisperma* Raf. (for *P. paucifolia* Willd.; an erroneous spelling of *Triclisperma* Raf.), yet chose not to recognize *Anthalogea* Raf. (for *P. polygama* Walt.) nor *Senega* Spach. (for *P. senega* L.), even though all of these

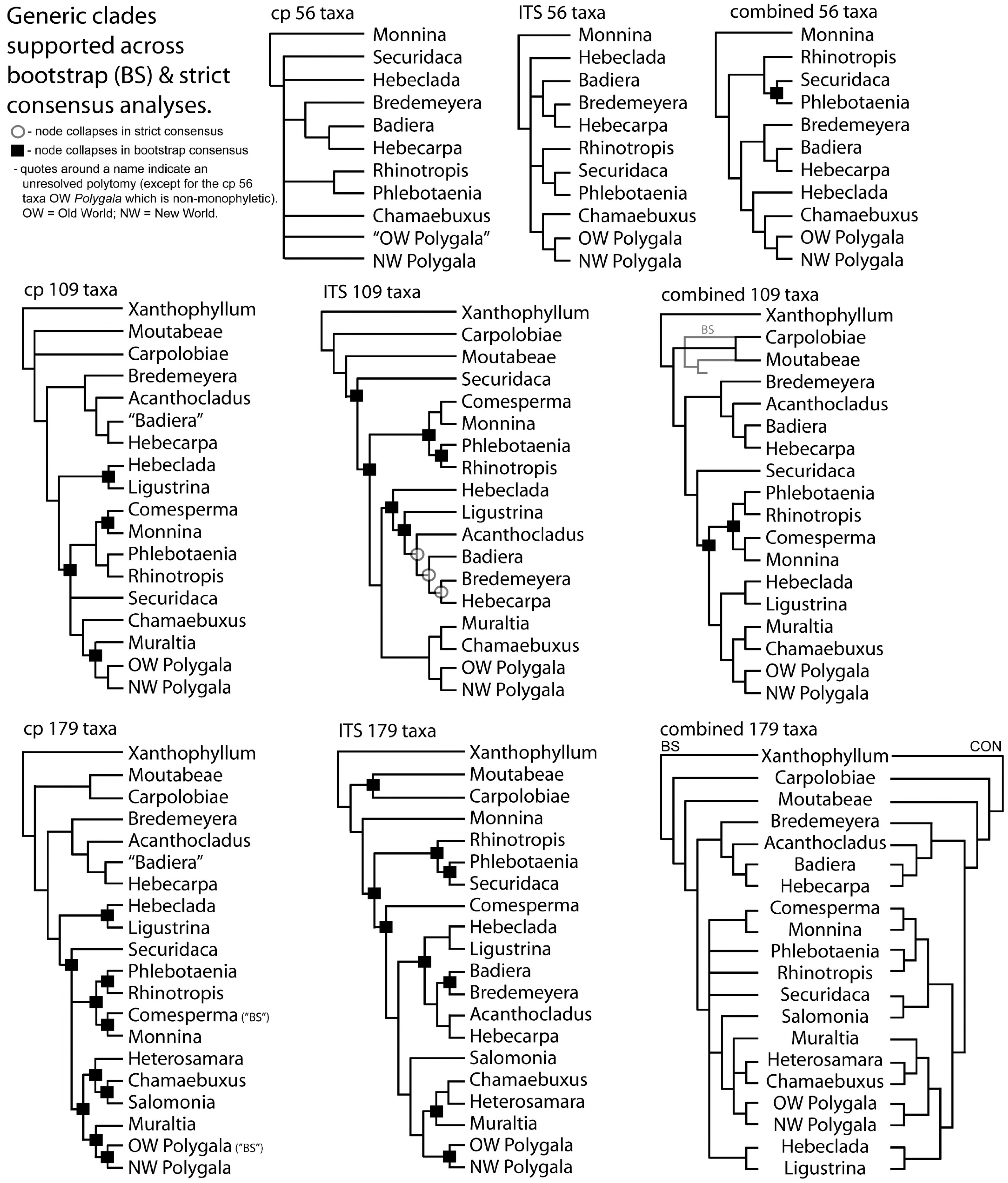

Fig. 1. Generic clades supported across bootstrap and strict consensus analyses, with combined chloroplast, nrITS, and combined nuclear and plastid results. The names here reflect traditional genera and subgenera of *Polygala*, thus, *Chamaebuxus* = *Polygaloides*, *Hebeclada* = *Asemeia*, and *Ligustrina* has not yet been elevated to generic rank.

groups have distinctive morphological features. Which genera to recognize was a matter of opinion, based on personal belief in which characters to stress as important and which author(s) to follow (e.g., Atran 1987; Stevens 1997). From a modern phylogenetic perspective, we now understand that *Asemeia* and *Polygaloides* (the correct name for *Triclisperma* once it is understood that the Old World species of *Polygala* subgenus *Chamaebuxus* s.str. are part of the same clade-based genus) are morphologically diagnosable clades phylo-

genetically distinct from other traditional *Polygala*. This is also true for two groups not treated as distinct by Small (1933), *Hebecarpa* and *Rhinotropis*, despite their morphological distinctiveness. The remaining 'genera' recognized by Small (1933) are subgroups of the New World *Polygala* clade and none of them can be maintained as genera without creating a blatantly artificial, non-monophyletic *Polygala* or overly splitting to recognize numerous additional genera, most of which could not be morphologically diagnosed as distinct from *Polygala*. Morphological distinctiveness has to be understood within a global phylogenetic context, and which clades to recognize as genera, while always inherently subjective, should nonetheless be constrained by the phylogenetic framework. Distinctive subclades can always be recognized as subgenera, without any compulsion to assign all species to a subgenus, i.e., the undesired situation of paraphyletic or polyphyletic genera can be circumvented while maintaining names for the more distinctive subgroups. Such an approach allows us to have taxonomy reflect phylogeny without ignoring distinctive subgroups nor obfuscating patterns of relationship by formally recognizing artificial assemblages of taxa that are not each other's closest relatives.

More than a century ago (Robinson 1906), botanists were warned about the dangers of describing artificial genera while focused on a geographically restricted flora and ignoring global patterns of variation among potentially related species. A regional approach to resolving relationships leads to confusion, overlapping circumscriptions, a lack of compatibility or comparability across floras, and taxonomic and nomenclatural instability (Robertson 1906). Higher level ranking is inherently subjective and was historically often rather arbitrary, primarily since there was no reliable, agreed-upon methodology for assessing patterns of evolutionary relationship. Now, phylogenetic hypotheses often provide a solid framework for the hierarchical grouping of species and understanding the interrelationships between groups, even though the importance of broad geographical sampling remains. Ultimately, as pointed out by Humphreys & Linder (2009), genera should be stable and predictive, as well as diagnosable and of a workable size, if possible, in order to be useful.

Over time, there have been shifts in how we conceive of genera and in the kinds of data we use to analyze them (Humphreys & Linder 2009). There has been much discussion and criticism of the Linnaean system and traditional type-based ranked names vs. phylogenetic naming systems, e.g., Benton (2000), Withgott (2000), Queiroz and Cantino (2001), Langer (2001), Berry (2002), Forey (2002), Nixon et al. (2003), Pickett (2005). Frustration with legalistic semantics and the arbitrariness of taxonomic rank can make alternative systems seem desirable. But, as pointed out by Moore (2003), even though our current system does use Linnaean conventions, it is not strictly bound by traditional ideas and is flexible and able to handle changing ideas. Names do not exist in a vacuum, they should and do imply something, and they are important for communication. Advances in our understanding should attempt to minimize taxonomic change when possible (Entwisle & Weston 2005), in order to minimize confusion and disruption of existing communication channels. But advances in our understanding do necessitate change for effective transmission of improved knowledge (Knapp et al. 2004).

Thus, since it is clear from my results (Fig. 1) and the work of others (Eriksen 1993a; Persson 2001; Forest et al. 2007) that *Polygala* s.l. is an artificial construct and must be recircumscribed, I have done so using names in accordance with the International Code of Botanical Nomenclature (McNeill et al. 2006) that provide historical continuity and minimize disruption. If only clades that are well-supported and morphologically diagnosable are named, then taxonomic stability can be achieved, although there is still often some room for interpretation. Nomenclatural codes are independent of taxonomic opinion, and it is important not to blur the lines between taxonomy and nomenclature (Dubois 2007), keeping in mind that true, lasting nomenclatural stability will only come from the quality science required to develop robust hypotheses (Knapp et al. 2004). Therefore, I have avoided renaming any suprageneric clades for now, as the relationships between the genera proposed herein are not yet robustly supported. Likewise, hypotheses of relationships of clades closest to the core group of *Polygala* are also not yet well understood, and much more work is needed to sort out which infrageneric groupings within *Polygala* s.str. will best reflect both morphology and phylogeny.

Monophyly is currently considered by most taxonomists to be the most important criterion for taxonomic changes (e.g., Backlund & Bremer 1998; Entwisle & Weston 2005; Judd et al. 2007). While phylogenetic studies can yield robust hypotheses of relationship with predictive power, it should be kept in mind that monophyletic groups are not necessarily predictive of overall similarity (just of shared derived similarity, e.g., Stevens 1985). Robustness of a clade, i.e., its persistence in new analyses and with the addition or deletion of taxa, should be well-documented before making taxonomic changes, as such robustness is an indication of the strength of the hypothesis that that group actually exists in nature (as a result of genealogical descent with modification). The results here are robustly supported, i.e., the clades I am recognizing are supported in all analyses, across all data sets and using double and triple the number of taxa (Fig. 1). These results also largely mirror those of other published phenetic (Paiva 1998) and phylogenetic analyses (Eriksen 1993a; Persson 2001; Forest et al. 2007), at least with respect to recognition of the clades named as generic groups here.

Some workers dismiss as inappropriate the idea that genera should be easy to recognize (Entwisle & Weston 2005) or write that the issue of convenience and utility is trivial (Stevens 1985). I agree that distinctive characters should not be emphasized nomenclaturally if they result in non-monophyletic groups (e.g., Pfeil & Crisp 2005), i.e., if the characters have been shown to be an artificial human construct not representative of shared ancestry they may still be useful for identification purposes but should not form the basis of formal classification. However, taxonomists need to keep in mind that classifications serve a user community, and considerations of recognizability, utility, and information retrieval, therefore, are important, at least as secondary criteria (Backlund & Bremer 1998; Judd et al. 2007).

The genera I propose here, *Asemeia*, *Hebecarpa*, *Polygaloides*, and *Rhinotropis*, are strongly supported in all the analyses, even when the relationship between the clades is NOT resolved (Fig. 1), they are morphologically diagnosable, and they make sense biogeographically. When there are alternative interpretations, such as combining sister clades, the biology of the organisms should be considered to determine which classification is most meaningful or useful, or makes the most sense in terms of diagnosable groups. For instance, Eriksen et al. (2000) circumscribed the genus *Badiera* to include *Polygala* subgen. *Hebecarpa* (Chodat) S.F. Blake on the basis of unpublished, preliminary data that suggested they were sister taxa, an hypothesis not yet supported by any other published analyses (e.g., Forest et al. 2007) and one that was formulated without any morphological context or detailed study of the species. Even though most of my analyses do support the hypothesis of *Badiera* and *Hebecarpa* as sister groups, it makes more sense morphologically to treat them as separate genera. Treating them as separate genera is also a more stable means of addressing the lack of robustness, i.e., all analyses support them as clades, but not all analyses support them as sister taxa, so lumping them entails an unnecessary taxonomic and nomenclatural risk, not to mention that there are not yet any known morphological synapomorphies for the putative *Badiera* + *Hebecarpa* clade, although each is independently a morphologically distinctive group that has been traditionally recognized.

The generic proposals provided here are not a reflection of personal opinion about which characters I think most represent the concept of a genus; instead, they reflect a phylogenetic approach to understanding relationships (based on DNA sequences), using morphology as a secondary guide/criterion for naming clades and ranking them within a taxonomic system (see Backlund & Bremer 1998; Judd et al. 2007), while also attempting to adhere to traditional names as much as possible. Even though all of the clades here given recognition as genera are morphologically diagnosable, it is often difficult to determine which features are synapomorphic for particular generic clades, especially when the characters are homoplasious. I hope in a future study to develop a detailed morphological matrix, so that morphological features can be explicitly mapped on to DNA-based as well as total evidence trees.

All the genera proposed here are traditionally recognized taxa (as subgenera or sections), and their recognition does not result in the paraphyly of any other genera. Conversely, to create a broadly circumscribed monophyletic *Polygala* would necessitate the inclusion of all other genera of Polygaleae! Despite the arbitrariness of rank, subsuming within *Polygala s.l.* a dozen or more distinctive generic clades such as the Asian mycoheterotrophs (*Epirixanthes* Blume and *Salomonia*), the pantropical samaroid lianas (*Securidaca*),

the primarily neotropical and mostly drupaceous shrubs (*Monnina*), etc., would do absolutely nothing to clarify our understanding of relationships within the tribe.

The species names transferred here (and the resulting new combinations) reflect my current understanding of the North American species, even though some of them are part of species complexes that could be split apart or treated more broadly. Some of the genetic polymorphisms detected in my phylogenetic analyses raise awareness of species-delimitation issues, e.g., at what point should distinctive populations be nomenclaturally recognized, but such issues must await monographic studies of the groups involved. In addition, all of the genera addressed here contain species outside of North America that are not being nomenclaturally transferred at this time, because the species have not been studied by me and because the primary purpose of this publication is to make the formal name changes required prior to using a name in the Flora North America treatment of Polygalaceae (Abbott, in review.).

Taxonomic Conclusions.—Paiva (1998) re-segregated the Old World genus *Heterosamara* and recognized 12 subgenera within *Polygala* s.l. My most complete cladistic analyses (Fig. 1), in congruence with other published analyses, show that eight of the subgenera of *Polygala* are more closely related to other genera than they are to subgenus *Polygala* and that *Polygala* subgen. *Brachytropis* (DC.) Chodat is phylogenetically nested within the subgen. *Polygala* s.str. The other two subgenera, *Polygala* subgen. *Chodatia* Paiva and *P.* subgen. *Gymnospora* (Chodat) Paiva, have been supported as distinct from *Polygala* s.str. in other published phylogenetic analyses (Forest et al. 2007). Thus, Paiva recognized many distinctive, morphologically defensible, monophyletic groups but maintained these (except *Heterosamara*) in an artificial, polyphyletic assemblage, *Polygala* s.l.

With respect to the circumscription of *Polygala* s.str. (as here circumscribed), the two primary concerns are that the relationships between the primarily Old World groups *Polygala* subgen. *Chodatia*, *Heterosamara*, and *Polygaloides* are not well-resolved, and that the New World and Old World clades of *Polygala* s.str. are not always supported as sister taxa. Taxon sampling for the group containing *Polygala* subgen. *Chodatia*, *Heterosamara*, and *Polygaloides* has been limited, but morphology does indicate that the three groups are distinctive. It is conceivable that *Polygala* s.str. could be expanded to include these three lineages, although results to-date suggest that this is unlikely and depends on the exact placement of the genera *Muraltia* and *Salomonia*.

North American Groups and Brief Biogeographic Discussion.—*Monnina* is represented by a single species in the U.S., *M. wrightii* A. Gray, in Arizona and New Mexico, representing the northern limit of a wider range in Mexico. *Monnina wrightii* also occurs disjunctly in Bolivia and Argentina, with single collections known from Peru and Uruguay (Eriksen 1993b). Eriksen hypothesized that the Mexican-United States population is likely the result of long-distance dispersal from the region of Bolivia-Argentina. My analyses show material from Bolivia does form a clade with material from Mexico, although there is some genetic divergence, suggesting that these populations may have been isolated for some time. My data show that the Central American species of *Monnina* do not form a clade, thus it seems clear that there have been multiple movements between the Andes and Central America. Most species of *Monnina* are shrubs with drupaceous fruits in the mountains of Central and South America, but *Monnina wrightii* is a member of a basal grade partially characterized by herbaceous habit and dry, flat, samaroid fruits. This group has been recognized generically as *Pteromonnina*, but Eriksen and Persson (2007), although citing unpublished, preliminary data suggesting the group is monophyletic, pointed out that the group is difficult to separate morphologically from other *Monnina* species. My cladistic analyses indicate that the species of *Pteromonnina* form a paraphyletic grade (*M. leptostachya* Benth., *M. stenophylla* A. St.-Hil., *M. tristaniana* A. St.-Hil., *M. wrightii*), not a clade, providing preliminary support for the conclusion that *Pteromonnina* should be included within *Monnina*. Amphitropical distribution patterns that span the neotropical lowlands are well-known in other groups of plants (e.g., Raven 1963; Solbrig 1972a, 1972b), and although many involve California and Chile (e.g., Morrell et al. 2000), some patterns are similar to that of *Monnina wrightii* (e.g., Holmes et al. 2008). Long-distance dispersal is accepted as the most likely scenario, but possible vectors and timing are not well understood.

All the remaining North American species of Polygalaceae traditionally have been treated as members of *Polygala*, with various, largely congruent, subgeneric and sectional classification schemes. The type species of *Polygala* is *P. vulgaris*, a polymorphic, widespread, mostly European taxon that has been reported as sparingly introduced in North America. *Polygala vulgaris* ranges natively to W Asia, with literature reports from N Africa that are likely based on errors or changed species concepts, as Paiva (1998) does not report this to be an African taxon. Using the criterion of monophyly, the only other species that can be maintained within *Polygala* are those that are phylogenetically supported as belonging to the same monophyletic group that contains *P. vulgaris*. Most of the North American taxa, although distantly related to the type, can be maintained within *Polygala*. Twenty North American species, though, corresponding to four different clades, are more closely related to other genera than they are to the type group of *Polygala*. All four of these clades correspond, at least in part, to traditionally recognized subgenera or sections that are morphologically diagnosable: *Asemeia*, *Hebecarpa*, *Polygaloides*, and *Rhinotropis*. The name *Asemeia* may not be as well-known as the name subgen. *Hebeclada*, just as *Polygaloides* is an obscure earlier name for subgen. *Chamaebuxus*, but the rules of nomenclature make it so that these names must be used at the rank of genus.

The four segregate genera proposed here can be separated from each other in North America by the following features. In the following discussion, the abbreviation "*P.*" refers to *Polygala*, the traditional genus for all the species. *Asemeia* and *Hebecarpa* have no beak or crest on their keel, and the sepals are free and caducous in *Hebecarpa*, while the two lower sepals are connate in *Asemeia*, and all the wings and sepals are persistent in fruit. The species of *Rhinotropis* have a cylindric or conic hollow beak on their keel (reduced or sometimes obscure to lacking in *P. acanthoclada* A. Gray, *P. intermontana* T. Wendt, *P. nudata*, and lacking in the extra-limital (non-U.S.) species *P. parryi* A.W. Benn. and *P. purpusii* Brandegee), five petals (the two lateral ones are much reduced and scale-like at base of staminal column), a persistent upper sepal (in the Lindheimeranae group, *P. desertorum* Brandegee, and *P. rusbyi* Greene; deciduous in others), the two lower sepals caducous (persistent in *P. desertorum* and *P. rusbyi*), and 7–8 stamens. For comparison, eight stamens is the normal condition in most North American species of *Polygala*, although seven stamens can rarely be found, and having only six stamens is reportedly the normal condition in two North American species, *P. nana* DC. and *P. paucifolia* (the latter treated here as *Polygaloides*). This variation within *Rhinotropis* is typical of how diagnostic, characteristic features that may be synapomorphic can still be homoplasious. *Polygala* and *Polygaloides* have a crest on their keel (there are a few extra-limital taxa without a crest), and the sepals are free and caducous in *Polygaloides*, while they are free (or rarely the lower two are united in extra-limital taxa) and persistent (rarely caducous) in *Polygala*, which often has more papery or membranous leaves. Additionally, the North American *Polygaloides paucifolia* is distinctive from North American *Polygala* by its low, creeping habit with only a few well-developed, relatively thin leaves near the apex of the erect stems, one to four large flowers (> 13 mm) in a terminal raceme with a very short peduncle, six stamens, and the occasional presence of cleistogamous flowers (only known elsewhere in North America from the three species of the *Polygala polygama* Walter complex and from two species of *Rhinotropis*).

Asemeia contains 25–30 species and occurs throughout Latin America, with only one species in the United States. There is a muddled taxonomic history associated with the name *Asemeia*, which originally led me to consider a proposal to have this name rejected. However, with proper lectotypification, *Asemeia* is the oldest available name for this group, since it can be argued that *Asemeia rosea* Raf. was provided as a new name for the invalid *Polygala pubescens* Nutt., which is a taxonomic synonym of *P. grandiflora* Walter. The details will be addressed in a forthcoming manuscript treating the genus (Pastore & Abbott, in prep) and another addressing the lectotypification of Nuttall names (Freire-Fierro, in prep). There are two deep clades within *Asemeia*, which correspond, at least in part, to the two sections recognized by Blake (1916) within *Polygala* subgen. *Hebeclada*, sect. *Apopetala* Blake and sect. *Adenotricha* Blake, which were separated primarily on the basis of flower size (larger in the *Apopetala* group). Aguiar et al. (2008) recognized 12 species (and seven varieties) in Brazil, but she did not treat sect. *Adenotricha* and sect. *Apopetala* as distinct. The single North American species, *P. grandiflora* Walter, is part of a widespread Latin American complex considered

to be related to *P. violacea* Aubl., and it is not clear how to separate it morphologically from some of the Latin American entities. Many workers, including Blake (1916, 1924) have recognized numerous segregate species out of *P. grandiflora* within the U.S. alone, while other workers have lumped all of them, including *P. grandiflora*, into *P. violacea* (e.g., Bernardi 2000). Preliminary molecular analyses (Abbott, unpublished data) suggest that *P. grandiflora* and *P. violacea* may not be each other's closest relatives. Molecular DNA analyses and observational field work suggest that the North American segregates can not reliably be segregated taxonomically and that *P. grandiflora* can only be included in *P. violacea* if several other currently recognized species are also synonymized, including many taxa considered by Brazilian workers to be distinct (e.g., Aguiar 2008). Therefore, I recommend that *P. grandiflora* be maintained apart from *P. violacea*, at least until there has been a detailed, robustly supported, comprehensive study of the complex. Restricted to the SE U.S. within North America, *P. grandiflora* may have moved in from Mexico during one of the hypsithermal intervals known to have brought western species into the southeast, or it may have spread into the southeast through Florida via the Caribbean.

Hebecarpa contains 40–70 species. Most species are Mexican, with a few extending into South America and nine extending into the SW U.S, five of which were included in my phylogenetic analyses. There are several species complexes in this group that are in serious need of revision, with overly fine, and perhaps meaningless, historical splitting (often based on only a single or a few specimens), so that the total number of species is probably fewer than 50. Chodat (1893) included the genus *Badiera* DC. as a subsect. in his sect. *Hebecarpa*, recognizing 25 species in subsect. *Euhebecarpa*, but *Badiera* has since been shown to be a distinctive clade separate from *Hebecarpa*, e.g., Forest et al. (2007) and my analyses (Fig. 1; Abbott 2009). Blake (1916) circumscribed three sections, three subsections, and two series within his subgen. *Hebecarpa*. One of the sections, sect. *Biloba* Blake, is now known to be part of the *Rhinotropis* group (Wendt 1978; Abbott 2009) and is discussed there. The monotypic sect. *Huateca* Blake, with the Mexican *P. tehuacana* Brandegee, has not been included in any phylogenetic analyses, so it should be tentatively viewed as incertae sedis, although morphological descriptions do suggest it belongs in *Hebecarpa*. Section *Hebecarpa*, which includes all of the North American species, was divided by Blake into three subsections, subsect. *Microthrix* Blake, subsect. *Hebantha* Blake, and subsect. *Adenophora* Blake. Subsection *Microthrix* contains seven of the North American species, one in ser. *Ovatifoliae* Blake (*P. ovatifolia* Gray), the others in ser. *Obscurae* Blake. Subsection *Hebantha* Blake was circumscribed with 34 species, none of them North American. Two of the three species of subsect. *Adenophora* range into North America, *P. greggii* S. Watson [= *P. glandulosa* Kunth] and *P. macradenia* A. Gray. My preliminary molecular DNA analyses suggest that subsect. *Adenophora* is sister to the rest of *Hebecarpa*. Final circumscription of subgroups must await additional study of more taxa. Species of *Hebecarpa* in the U.S. are largely restricted to (semi-)arid regions of the southwest, representing contiguous northern expansions of their ranges in Mexico, which is the center of diversity for this group. A few species range into Central America and Andean South America, but they are not the basal-most species, suggesting that they have arrived in these regions secondarily.

Polygaloides contains six or seven species globally and corresponds to subsection III of Chodat's (1893) *Polygala* sect. *Chamaebuxus*, plus one species unplaced by him to subsection, *P. paucifolia*, disjunct in northern North America from the remaining five or six species in Europe and northern Africa. This North American species is isolated and morphologically distinct from its closest relatives in Europe and northern Africa, perhaps as a vicariant relict of a historical circumboreal flora. While its creeping herbaceous habit with relatively thin leaves and large showy crest set the North American taxon apart from the Old World taxa [subshrubs or shrubs to 1 m tall with subcoriaceous leaves and small, fairly inconspicuous crest], the form of the stigma, the glanduliform disc at the base of the flower, and the few-flowered inflorescences morphologically unite the taxa (Chodat 1893). No existing descriptions for this *Polygaloides* group are entirely accurate, as, based on phylogenetic analyses, they all include elements that are not part of this clade or exclude species that are, e.g., in Blake (1916) the only species treated in the *Chamaebuxus* group were those belonging to the group here recognized as *Rhinotropis*, with no reference to the Old World species, nor to *P. paucifolia*. Blake (1924)

later circumscribed *P. paucifolia* as the sole member of the *Triclisperma* group, presumably as a section of *Chamaebuxus* or as a subsection of *Rhinotropis*, but rank was not explicitly stated. Paiva's (1998) description of *Chamaebuxus* makes no mention of the North American taxon. Although it is easy enough to contrast the distinctiveness of the single North American taxon against the remaining taxa in North America, more work is needed to carefully study the morphological differences between all species of *Polygaloides* and *Polygala*, as well as the closely related Old World groups *Chodatia*, *Heterosamara*, *Muraltia*, and *Salomonia*, as much of the information provided by others, e.g., Blake (1916) and Chodat (1893, 1896), just has not been carefully reviewed with this limited group of taxa in mind. Unfortunately, Rafinesque's description of *Triclisperma*, just as with Haller's (1768) description of *Polygaloides*, is not unique enough to differentiate this taxon from *Polygala*, i.e., based on their descriptions alone, there is no reliable morphological basis for determining which other taxa could or should actually be included in the clade that contains *Polygaloides* and *Triclisperma*, together a small subset of the traditional *Chamaebuxus* group recognized by Chodat (1893).

Von Haller (1768), in his early account of the plants of Switzerland, recognized one species [*Polygala chamaebuxus* L. = *Chamaebuxus alpestris* Spach = *Polygaloides chamaebuxus* (L.) O. Schwarz], using a polynomial description, as different from *Polygala* based on its lack of flabelliform ornamentation and three-parted calyx. The crest on the keel is not as conspicuous as in the other Swiss species of *Polygala* but is still present, and the three-parted calyx is not actually any different from other *Polygala*—Haller's own description of *Polygala* refers to its three-parted calyx; it's just that the wings (lateral petaloid sepals) are much larger and showier in this species than in other European taxa, so are less obviously sepals. In essence, there is nothing in Haller's description that actually diagnoses *Polygaloides* as distinct from *Polygala*. Although nomenclaturally irrelevant, I point out that Haller did not actually present his treatment as if he were describing a new genus; he was merely citing the pre-Linnaean work of others. The group was recircumscribed by A.P. de Candolle (1824) as *Polygala* sect. *Chamaebuxus* DC., then re-elevated to generic status, as *Chamaebuxus*, by Spach (1839), and then returned to sectional status by Chodat (1893), although in an expanded sense with three informal subgroups (two of which correspond to *Rhinotropis* and a group of species now recognized as part of the *Chodatia* or *Heterosamara* clades). Duchartre (1847) then transferred the group to *Polygala* subgen. *Chamaebuxus*, the rank later followed by Blake (1916), who erroneously thought he was the first to describe it as a subgenus, and by Paiva (1998). Since names only have priority at a given rank and neither *Chamaebuxus* nor *Triclisperma* have been any more widely used as a genus name than *Polygaloides*, it seems most parsimonious just to accept the earliest validly published name, *Polygaloides* Haller, especially since most of the taxa in the group have already had combinations made in that genus (Schwarz 1949).

A proposal to conserve *Chamaebuxus* against *Polygaloides* (Janchen 1953) was rejected (Rickett 1958), but the specific proposal rejected was to conserve *Chamaebuxus* Spach over *Polygaloides* Agosti, not *Polygaloides* Haller. It was ruled that Agosti's names were not validly published, thus conservation against an invalid name would have been superfluous. Since *Polygaloides* Agosti is the same name and is based on the same type species as *Polygaloides* Haller, had *Polygaloides* Agosti been validly published, it would still have been of no nomenclatural significance, as a later isonym. Potentially, then, a proposal could be re-attempted to conserve the more familiar name *Chamaebuxus*, but its wider usage has been at infrageneric rank only. As a genus, *Chamaebuxus* has been as little used as *Polygaloides*, providing no impetus to argue for its conservation. Such a proposal would not only need to see the conservation of *Chamaebuxus* Spach against *Polygaloides* Haller but also against *Triclisperma* Raf., another obscure, little-used, but validly published name. Rafinesque established the monotypic North American genus *Triclisperma* (1814), which modern phylogenetic studies (Abbott 2009) have shown is clade-forming with Old World *Polygaloides* [= *Polygala* subgen. *Chamaebuxus* s.str.]. Rafinesque wrote that the name derives from the seeds with three valves (referring to the three-lobed aril, presumably). Since he didn't mean hair by "Tric(h)-," later workers attempting to 'correct' the name as *Trichlisperma* were in error, e.g., Nieuwland (1914) & Small (1933). Rafinesque had erroneously created his own new specific epithet (*T. grandiflora* Raf.), when he should have used the existing epithet *paucifolia*. That nomenclatural error was rectified by Nieuwland (1914), who made the combination *Triclisperma paucifolia* (Willd.) Nieuwl.

Rhinotropis contains 17 species, all in SW United States and Mexico (a single species, *P. purpusii*, extends into Guatemala), 13 ranging into the SW U.S., nine of which were included in my phylogenetic analyses (Abbott 2009). Of all the groups treated here, this is the only one that has been explicitly monographed within the last 100 years (Wendt 1978). Blake (1916) treated this group as a section within subgen. *Chamaebuxus* and divided it into the monotypic subsect. *Pantomone* Blake (*P. desertorum*) and subsect. *Eurhinotropis* Blake. Wendt (1978) discarded Blake's subsectional classification, dividing sect. *Rhinotropis* into three series: ser. *Californicae* T. Wendt, ser. *Intermontanae* T. Wendt, and ser. *Lindheimeranae* T. Wendt. Wendt included the species treated by Blake (1916, 1924) as sect. *Biloba* (of subgen. *Hebecarpa*) within his ser. *Lindheimeranae*. Section *Biloba* has two species, *P. purpusii* and *P. parryi*, neither in North America north of Mexico. These species were not traditionally considered to be part of *Rhinotropis* because of their beak-less keel, but some members of *Rhinotropis* can also have an obscure (to rarely lacking) beak, flowers of *P. purpusii* do rarely develop an obscure beak, and all other features support their inclusion (Wendt 1978). My molecular DNA analyses (Abbott 2009) confirm that *P. purpusii* is not part of *Hebecarpa*, but a member of *Rhinotropis*, corroborating Wendt's placement within the ser. *Lindheimeranae* clade. *Rhinotropis* is probably sister to the Caribbean clade *Phlebotaenia*, and it also appears to be fairly closely related to the pantropical (although predominantly Neotropical) genus *Securidaca*. *Rhinotropis* is largely endemic to arid regions of SW North America and Mexico, where it appears to have evolved, but some species, especially the phylogenetically basal ones, do occur in mesic areas.

Even with the recognition of all the distantly related clades as separate, segregate genera, *Polygala* s.str. still contains a few hundred species and has a nearly cosmopolitan distribution, including the remaining North American species. Relationships within *Polygala* s.str. will be discussed in a forthcoming publication.

NEW COMBINATIONS AND CHANGES OF STATUS

Asemeia Raf., Herb. Raf. 80. 1833 [late 1833 or early 1834]. Type species: *Polygala grandiflora* Walter.

= *Polygala* L. sect. *Hebeclada* Chodat, Mém. Soc. Phys. Genève 31, pt. 2, no. 2:43. 1893. *Polygala* L. subgen. *Hebeclada* (Chodat) S.F. Blake, Contr. Gray Herb. 47:59. 1916. Type species: *Polygala hebeclada* DC.

Asemeia grandiflora (Walter) Small, Man. SE Fl. 766. 1933. *Polygala grandiflora* Walter, Fl. Carol. 179. 1788.

Hebecarpa (Chodat) J.R. Abbott, comb. et stat. nov. *Polygala* L. sect. *Hebecarpa* Chodat, Mém. Soc. Phys. Genève 31(2):9. 1893. *Polygala* L. subgen. *Hebecarpa* (Chodat) S.F. Blake, Contr. Gray Herb. 47:17. 1916. Type species: *Polygala obscura* Benth.

Hebecarpa barbeyana (Chodat) J.R. Abbott, comb. nov. *Polygala barbeyana* Chodat, Mém. Soc. Phys. Genève 31(2):16. 1893.

Hebecarpa greggii (S. Wats.) J.R. Abbott, comb. nov. *Polygala greggii* S. Wats., Proc. Amer. Acad. Arts 17:325. 1882. [*Polygala glandulosa* Kunth, Nov. Gen. Sp. 5:404. 1823, nom. illeg.]

Hebecarpa macradenia (A. Gray) J.R. Abbott, comb nov. *Polygala macradenia* A. Gray, Smithsonian Contr. Knowl. 3:39. 1852.

Hebecarpa obscura (Benth.) J.R. Abbott, comb. nov. *Polygala obscura* Benth., Pl. Hartw. 58. 1840.

Hebecarpa ovatifolia (A. Gray) J.R. Abbott, comb. nov. *Polygala ovatifolia* A. Gray, Smithsonian Contr. Knowl. 3:39. 1852.

Hebecarpa palmeri (S. Watson) J.R. Abbott, comb. nov. *Polygala palmeri* S. Watson, Proc. Amer. Acad. Arts 17:325. 1882.

Hebecarpa rectipilis (S.F. Blake) J.R. Abbott, comb. nov. *Polygala rectipilis* S.F. Blake, Contr. Gray Herb. 47:27. 1916.

Polygaloides Haller, Hist. Stirp. Helv. 1:149. 1768. *Chamaebuxus* (DC.) Spach, Hist. Nat. Veg. 7:125. 1839. *Polygala* L. sect. *Chamaebuxus* DC., Prod. 1:331. 1824. *Polygala* L. subg. *Chamaebuxus* (DC.) Duch. in Orbigny, Dict. Univ. Hist. Nat. 10:381. 1849. Type species: *Polygala chamaebuxus* L.

Polygaloides paucifolia (Willd.) J.R. Abbott, comb. nov. *Polygala paucifolia* Willd., Sp. Pl. 3(2):880. 1802.

Rhinotropis (S.F. Blake) J.R. Abbott, comb. et stat. nov. *Polygala* L. sect. *Rhinotropis* S.F. Blake, Contr. Gray Herb. 47:70. 1916. *Polygala* L. subgen. *Rhinotropis* (Blake) Paiva, Fontqueria 50:148. 1998. Type species: *Polygala lindheimeri* A. Gray.

Rhinotropis acanthoclada (A. Gray) J.R. Abbott, comb. nov. *Polygala acanthoclada* A. Gray, Proc. Amer. Acad. Arts 11:73. 1876.

Rhinotropis californica (Nutt.) J.R. Abbott, comb. nov. *Polygala californica* Nutt., Fl. N. Amer. 1:671. 1840.

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Rhinotropis lindheimeri (A. Gray) J.R. Abbott, comb. nov. *Polygala lindheimeri* A. Gray, Boston J. Nat. Hist. 6:150. 1850.
Rhinotropis lindheimeri (A. Gray) J.R. Abbott var. **eucosma** (S.F. Blake) J.R. Abbott, comb. nov. *Polygala eucosma* S.F. Blake, Contr. Gray Herb. 47:72. 1916.
Rhinotropis lindheimeri (A.Gray) J.R. Abbott var. **parvifolia** (Wheelock) J.R. Abbott, comb. nov. *Polygala lindheimeri* A. Gray var. *parvifolia* Wheelock, Mem. Torrey Bot. Club 2:143. 1890.
Rhinotropis madrensis (T. Wendt) J.R. Abbott, comb. nov. *Polygala madrensis* T. Wendt, Lundellia 5:27. 2002.
Rhinotropis maravillasensis (Correll) J.R. Abbott, comb. nov. *Polygala maravillasensis* Correll, Wrightia 3:131. 1965.
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Rhinotropis nitida (Brandegee) J.R. Abbott var. **tamaulipana** (T. Wendt) J.R. Abbott, comb. nov. *Polygala nitida* Brandegee var. *tamaulipana* T. Wendt, J. Arnold Arbor. 60:508. 1979.
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BOOK REVIEW

Michel Poulain, Marianne Meyer, and Jean Bozonnet, Text in French with translation of glossary and keys to identification into English by Annie Kohn. 2011. **Les Myxomycètes: Guide to Identification.** (ISBN: 978-209518540-2-4, EAN: 9782951854024, pbk.). La Fédération Mycologique et Botanique Dauphiné-Savoie. (**Orders:** www.fmbds.org; tresorier@fmbds.org). €120.00, 568 pp. (Vol. 1), 544 pp. (Vol. 2), 675 color images, 556 b/w line drawings mostly microscopic structures, 9½" × 6¾".

The superb habit photography of myxomycete fruiting bodies is the hallmark of this book. The depth of field of tiny stalked sporangia exemplified by the genera *Cribraria* and *Licea* is unsurpassed by any other publication. Indeed, this is the only publication that has so many tiny sporangia in sharp focus that results from composition and orientation of specimens and camera equipment to illustrate these species. True color renditions show the brilliant hues and dehiscent patterns of the peridial surfaces as well as the iridescent colors seen in genera such as *Diachea*, *Elaeomyxa*, and *Lamproderma*. These color images show enough morphological detail (1.0 to 430× given for individual magnification) to picture-key many more species not adequately illustrated or not included in other myxomycete publications. The author's contributions through photography are impressive and raise the beauty of these life forms to an aesthetic art form. An informative section would have been welcomed on how to duplicate the color images with a description of the photographic technique and equipment used over a lifetime of myxomycete collecting.

Most color habit illustrations occupy half a page and black and white line drawings in the other half showing microscopic features of the capillitium (when present) and spore shape and ornamentation. Line drawings are illustrated at 200 to 2000× magnifications, and for spore ornamentation, a compound microscope will require an oil immersion optical lens system. Scanning electron micrographs of the peridium, capillitium or spore ornamentation were not included. Captions for illustrations are in French. All of the taxa illustrated are based on specimens deposited in the private herbarium of Marianne Meyer in France that numbers more than 35,000 specimens.

The illustrations are grouped by orders: Liceales, Echinosteliales, Trichiales, Physarales, and Stemonitales and arranged so taxa closely related are next to each other rather than alphabetically. This is problematic in view of the fact that in too many cases morphological similarity may not represent phylogenetic relationships. However, an index for volume 2 is arranged alphabetically with boldface numbers corresponding to each illustration. The standard numbers in volume 2 correspond to page numbers in the French keys in volume 1 and italics numbers correspond to page numbers in the English keys.

Volume 1 is divided into a part in French (pp. 7–31) that includes the Preface, Introduction, Acknowledgments, Biology of Myxomycetes, Classification, Ecology, Collections, Deposition in Herbaria, and Microscopy. A Glossary and Identification Keys make up the rest of the French portion (pp. 23–287). The Preface, Glossary, and Identification Keys (pp. 289–550) are translated into English that will increase the value of this volume to a larger readership.

The glossary of descriptive terms with illustrations is helpful in understanding the keys to the species. The use of the traditional term limy is used for calcium carbonate deposits in the myxomycetes. However, the definition and use of myxocarp, sporocarp, and sporocyst are created for more familiar terms such as fruiting body, sporangia, and spore case. Several new terms such as a basal columella with line drawings that illustrate a secondary columella, hypocolumella, and filamentous columella aid in expanding the lexicon of myxomycete terminology. Keys to the orders, families, genera, species, and varieties include 853 taxa (530 illustrated) of myxomycetes. The bibliography is not comprehensive and includes mostly European references.

These three authors have devoted most of their lives to the study of the nivicolous (snow) myxomycetes concentrated mostly in the European Alps located primarily in France and neighboring countries. These volumes are the best source of information on this group of myxomycetes found mostly in mountainous regions of the world. The classification of families, genera, and more use of varieties follows more narrow European species concepts not followed by all myxomycete taxonomists. The genus *Meriderma* is validated and species given descriptions but without a discussion that includes the morphological character states that segregate this taxon from other closely related taxa in the genus *Lamproderma*.

Dichotomous keys are based on morphological characters that may be variable such as color, size, and ornamentation. This always has been problematic involving the identification of myxomycete species. Genera with greater number of species such as *Arcyria, Cribraria*, *Didymium*, *Licea*, and *Physarum*, for example, are divided into different groups and keys. This would appear to facilitate identification; however, there is no indication that the keys included here were tested and used over time. These books are oversized and too weighty for extensive use in the field or to carry in a backpack. The spine appears to be solidly bound but time will tell if regular use will keep pages intact.

Myxomycetes have piqued the curiosity of naturalists for more than 300 years especially the brilliant color arrays displayed by the developing and mature fruiting bodies visible to the unaided eye. The photography recorded here highlights the fantastic beauty of myxomycetes unmatached in any other publication and for that reason alone these books should be purchased. The cost is reasonable for the most authoritative treatment of nivicolous myxomycetes. The general public has many choices of books devoted to nature, but this one should be at the top of the list for anyone with even a passing interest in myxomycetes. Professional and amateur mycological society members, mycologists, myxomycologists, national parks and conservation agencies, college, university, and public libraries, and ecologists interested in nivicolous habitats will want to have these books on their bookshelf.—*Harold W. Keller, Research Associate, Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107-3400, U.S.A.*

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NEW COMBINATIONS IN *PHORADENDRON LEUCARPUM* (VISCACEAE)

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ABSTRACT

Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. is the nomenclaturally correct binomial for American mistletoe in the United States and Mexico. Several western taxa have been included as taxonomic synonyms of this species, with recognition as subspecies within *P. serotinum*. We propose here the necessary nomenclatural combinations to make available the subspecific taxa within *P. leucarpum*.

Key Words: Nomenclature, *Phoradendron leucarpum, Phoradendron serotinum,* Viscaceae

RESUMEN

Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. es el nombre nomenclaturalmente correcto para el muérdago americano en los Estados Unidos y México. Varios taxa occidentales han sido incluidos como sinónimos taxonómicos de esta especie, con el reconocimiento como subespecies dentro del *P. serotinum*. Proponemos aquí las combinaciones nomenclaturales necesarias para hacer disponibles los taxa subespecíficos dentro del *P. leucarpum*.

Palabras Claves: Nomenclatura, *Phoradendron leucarpum, Phoradendron serotinum,* Viscaceae

Reveal and Johnston (1989) established *Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. as the nomenclaturally correct name for American mistletoe, a species native to the United States and Mexico, based on a 1817 collection from the Carolinas. Initially, Rafinesque gave two binomials for American mistletoe: *Viscum leucarpum* in 1817 and *V. serotinum* in 1820 (Reveal and Johnston 1989). Johnston (1957) made the combination *Phoradendron serotinum* (Raf.) M.C. Johnst. for American mistletoe because he considered the specific epithets "*leucarpum*" and "*leucocarpum*" to be orthographic variants. Brummitt (1988) reported a ruling from the Committee for Spermatophyta that *Phoradendron leucarpum*, an eastern United States species, and *P. leucocarpum*, a Peruvian species, were not homonyms. Following Brummitt (1988) and the rule of priority, Johnston's (1957) combination became a synonym. Distinctive *Phoradendron* taxa ranging from Texas to California to Oregon, and into Mexico have variously been proposed as infraspecific entities under epithets other than "*leucarpum*," e.g., "*serotinum*," or as distinct species (Wiens 1964; Kuijt 2003). Despite the conclusions reached in the 1989 article, the most recent monographer of *Phoradendron* (Kuijt 2003) did not use the correct binomial *P. leucarpum*. Consequently, for workers who want to accept Kuijt's taxonomic judgment, the correct nomenclatural combinations for infraspecific taxa within *P. leucarpum* do not exist.

The choice of which name(s) to use for American mistletoe has been the source of much taxonomic and nomenclatural contention during the last century, as discussed by Kuijt (2003). Prior to 1989, *Phoradendron serotinum* was hardly uncontested, so there is a history of mixed usage, which is not just about nomenclature but also taxonomic judgment. We are not challenging Kuijt's taxonomic judgment; we accept the entities and ranks as he defined them. Our goal is to provide the correct scientific name, *Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. in combination with Kuijt's infraspecific taxa as we understand them.

Major post-2003 national and international online databases accept *Phoradendron leucarpum* (i.e., GRIN, USDA, ARS, National Genetic Resources Program 2010; The International Plant Names Index 2010; PLANTS Database, USDA, NRCS 2010), as do numerous publications on a wide variety of themes, e.g., general parasite

papers, mistletoe studies, state floras and atlases, many state floristic inventories, and general references on medicinal, toxic, or insect host plants.

Nickrent et al. (2010) submitted a proposal to conserve *Phoradendron serotinum* over *P. leucarpum*, or technically the basionym *Viscum serotinum*, based on common usage, necessity of herbarium annotations, and avoidance of making new infraspecific combinations, but they admitted that "Given the 1988 Committee for Spermatophyta decision on parahomonymy, it is undeniable that the correct name for this species in *Phoradendron* is *P. leucarpum*." In our judgment, abandonment of the correct binomial, *P. leucarpum,*is unwarranted given the correct combination by Reveal and Johnston (1989). We believe the Nomenclature Committee for Vascular Plants should not recommend acceptance of the proposal.

NEW SUBSPECIFIC COMBINATIONS

Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. subsp. **leucarpum,** Taxon 38:107. 1989. Basionym: *Viscum leucarpum* Raf., Fl. Ludov. 79. 1817. Type: U.S.A. Carolinas: without date, *Walter s.n.* (lectotype, designated by Reveal & Johnston 1989: BM).

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Phoradendron serotinum (Raf.) M.C. Johnst., Southw. Naturalist 2:45. 1957.

Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. subsp. **angustifolium** (Kuijt) J.R. Abbott & R.L. Thompson, comb. nov. Basionym: *Phoradendron serotinum* (Raf.) M.C. Johnst. subsp. *angustifolium* Kuijt, Syst. Bot. Monogr. 66:418. 2003. Type: MEXICO. Durango: Cerro Chupadero, 35 SE of El Salto, just W of Pueblo Nuevo, 2000–2500 m, on *Quercus durifolia*, *Maysilles 8059* (holotype: NY; isotypes: MEXU, MICH).

Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. subsp. **macrophyllum** (Engelm.) J.R. Abbott & R.L. Thompson, comb. nov. Basionym: *Phoradendron flavens* [as *flavescens*] (Pursh) Nutt. ex A. Gray var. *macrophyllum* Engelm., Rep. U.S. Geogr. Surv., Wheeler 6 (Botany):252. 1878. Type: U.S.A. Arizona. Pinal Co.: Camp Grant (near junction of Gila and Bonita rivers), 5500 ft, on *Fraxinus*, *Rothrock 362* (lectotype, designated by Wiens 1964: MO).

Phoradendron macrophyllum (Engelm.) Cockerell, Amer. Naturalist 34:293. 1900. *Phoradendron serotinum* (Raf.) M.C. Johnst. var. *macrophyllum* (Engelm.) M.C. Johnston, Southw. Naturalist 2:46. 1957.
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Phoradendron tomentosum (DC.) Engelm. ex. A. Gray var. *macrophyllum* (Engelm.) L.D. Benson, Trees Shrubs Southw. Deserts 286. 1981.
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Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst. subsp. **tomentosum** (DC.) J.R. Abbott & R.L. Thompson, comb. nov. Basionym: *Viscum tomentosum* DC., Prodr. 4:670. 1830. Type: MEXICO. San Luis Potosí: Real de Catorce, on *Mimosa*, *Berlandier 1364* (holotype: G; isotypes: MO, P).

Phoradendron serotinum (Raf.) M.C. Johnst. subsp. *tomentosum* (DC.) Kuijt, Syst. Bot. Monogr. 66:423. 2003.
Phoradendron tomentosum (DC.) Engelm. ex A. Gray subsp. *tomentosum* Mem. Amer. Acad. Arts Ser. 2, 4(1):59. 1849.
Phoradendron flavens [as *flavescens*] (Pursh) Nutt. ex A. Gray var. *tomentosum* (DC.) Engelm. in Brewer & Watson, Bot. Calif. 2:105. 1880.

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BOOK REVIEW

Tom Butler (Essays), Antonio Vizcaíno (Photography), and Tom Brokaw (Foreword). 2008. **Wildlands Philanthropy: The Great American Tradition.** Deluxe edition with slipcase, also includes bonus DVD, featuring a narrated slideshow with stories and images from Wildlands Philanthropy. (ISBN-13: 978-1-60109-020-1, ISBN-13: 978-1-60109-019-5, hbk.). Earth Aware Editions, 17 Paul Drive, San Rafael, California 94903, U.S.A. (**Orders:** www.insighteditions.com; 415-526-1370; 415-526-1394 fax). $125.00 (US), $141.50 (Canada), 352 pp., 170 color photos in large-format design, 17.23" × 14.25".

This is a weighty big book in size, in pounds, in panoramic landscape images, and in narrative content. The spectacular photographic images (170) by Antonio Vizcaíno capture the unrivaled beauty of "mother nature" all in the category of "you have to see it to believe it". This book is about American philanthropists and the places they saved. The Foreword by Tom Brokaw gives his personal account of his appreciation of wild places growing up in South Dakota. The brief narratives by Tom Butler capture the essence of each place. The six-page introduction provides a definition of wilderness and a historical context for the conservation movement. Individual stories document the different rationales for saving wild places based on aesthetic beauty or a sense of place that spans time immemorial for future generations. This book champions the individual donors who gave of their time and wealth to protect biodiversity and landscape vistas.

Each narrative of the included areas (39) is preceded by a black and white portrait of the benefactors who helped with their volunteer efforts and philanthropy. The scope of the areas are in the Americas from Alaska to Tierra del Fuego and include: National Monument (1), State Parks (7), National Parks (6), Research/Temperate Forests (3), Sanctuaries (4), Preserves (2), Wilderness (1), Research Ranch (1), Islands (2), South America (6) Mexico (1), National Wildlife Refuge/Centers (3), Tropical Forest (1), South America areas (6) among others.

Several examples of stories that represent different ecological regions and parts of different countries will serve to highlight some of the preserved areas. Texans will appreciate the recognition of Guadalupe Mountains National Park (86,000 acres) located in western Texas and southern New Mexico that highlights the philanthropy of Wallace Pratt (1885-1981). He dedicated much of his life to the preservation of McKittrick Canyon, the surrounding Guadalupe Mountains and the Chihuahuan Desert. Two-page spreads of landscape color vistas show the mountains in the background with riparian trees, and desert grasses and flowers in the foreground, another setting with sand dunes in the foreground, and still another more focused on desert blooming flowers that impart a kaleidoscope of colors so typical of desert areas after recent rains. Konza Prairie Biological Station (Katherine Ordway's Tallgrass Preserve) represented the first system of tallgrass prairie preserves near Manhattan, Kansas that also is now part of a Long Term Ecological Research project funded by the National Science Foundation. One of the oldest mountain systems in the world with one of the highest species diversity in a temperate region is the Great Smoky Mountains National Park or The People's Park. John D. Rockefeller Jr.s' gift along with the people of Tennessee and North Carolina saved this area from the logger's ax during the Great Depression so that visitors today can enjoy the largest tract of old growth broadleaf deciduous forest in eastern United States of America. Área de Conservación Guanacaste represents the restoration of a dry tropical forest as part of a pioneering research project by Daniel Janzen and Winnie Hallwachs in Costa Rica. The efforts of Kristine McDivitt Tomkins to preserve Monte León National Park (Patagonia Wild) in Argentina saved part of the Patagonian steppes and wildlife.

Corcovado National Park (Beacon of Wildness) saved by Douglas Tomkins and Peter Buckley, and given away to the Chilean government to become a national park, is one of the most spectacular wilderness and roadless areas left on Earth.

The Afterword (The Donors No One Knew) has many examples of anonymous donors who gave land acquisitions for public preservation. The largest addition of private property for public ownership in U.S. history (600,000 acres) included desert areas of California especially in Joshua Tree National Park. The Bibliography has 67 references, mostly books, published in the last 20 years that relate to areas noted in the text. A section titled Land Conservation Resources contains contact information about conservation land trusts for people interested in getting involved with the protection of open space, agricultural lands, and natural areas. This book should be in the collection of organizations both private and public such as nature conservancies, visitor centers at national and state parks, state natural resource agencies, public and university libraries, individuals with a passion to protect tracts of land, and law firms, institutes and centers. The prohibitive cost of publishing large-format books on a grand scale like this one may become a thing of the past with cheaper online options so the Foundation for Deep Ecology merits special thanks for their financial support of books dedicated to the preservation of wild areas for future generations.—*Harold W. Keller, Research Associate, Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107-3400, U.S.A.*

TYPIFICATION AND SYNONYMY OF THE SPECIES OF *EUPHORBIA* SUBGENUS *ESULA* (EUPHORBIACEAE) NATIVE TO THE UNITED STATES AND CANADA

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ABSTRACT

This paper reviews and establishes the types and current synonymy of the 17 species of *Euphorbia* L. subgenus *Esula* Pers. that are native to the area covered by the *Flora of North America*. Neotypes are designated for *Agaloma purpurea* Raf., *Euphorbia longicruris* Scheele, and *E. roemeriana* Scheele, and lectotypes are designated for other names that are treated as accepted species or as synonyms in this treatment. The affinities of the North American species are discussed, particularly in relation to Eurasian members of subgenus *Esula*.

RESUMEN

Este trabajo revisa y establece los tipos y sinonimia actuales de las 17 especies de *Euphorbia* L. subgénero *Esula* Pers. que son nativas al área cubierta por la obra *Flora of North America*. Se designan neotipos para *Agaloma purpurea* Raf., *Euphorbia longicruris* Scheele, y *E. roemeriana* Scheele, y se designan lectotipos para otros nombres tratados aquí como especies aceptadas o como sinónimos. Las afinidades de las especies norteamericanas se discuten, especialmente en relación a los taxa euroasiáticos del subgénero *Esula*.

INTRODUCTION

Euphorbia L. subgenus *Esula* Pers. contains approximately 470 species, with the majority of the species occurring in temperate Eurasia. There are also several smaller, disjunct centers of diversity in areas such as Macaronesia, the East African mountains, South Africa, and the New World. This group was formerly recognized by some botanists as the separate genus *Tithymalus* Gaertn. (e.g., Klotzsch 1860; Small 1903; Chrtek & Křísa 1982, 1992), but it is generally maintained within *Euphorbia*. Molecular phylogenetic studies (Steinmann & Porter 2002; Bruyns et al. 2006; Kryukov et al. 2010; Zimmermann et al. 2010) have shown that the subgenus corresponds to one of four major clades within the genus, and the latest results, using multiple markers from all three plant genome compartments, confirm that it is the sister group to the other three subgenera (Horn et al. 2009).

Euphorbia subgenus *Esula* is represented in the continental United States and Canada (the area covered by the *Flora of North America* project) by 17 native species and 15 naturalized Eurasian species. The only paper dealing specifically with the North American species is Norton (1899), where he described several new infraspecific taxa and followed the infrageneric classification system of Boissier (1862). There have been no further attempts since then to systematize the nomenclature of this group, discuss possible relationships to Eurasian species, or place the North American species in more recent infrageneric classifications, such as those of Prokhanov (1949, 1964) and Geltman (2007).

This paper is part of a global initiative to update the systematics of *Euphorbia* worldwide (Berry & Riina 2007; Esser et al. 2009), and it is also a precursor to the treatment of *Euphorbia* for the *Flora of North America*

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(FNA) project. Here we aim to systematize the nomenclature and typification of the native North American species of subgenus *Esula* and to provide a discussion of their relationships with Eurasian taxa.

METHODS

Holdings of several North American (DWC, GH, KSC, MICH, MO, NY, RM, US) and European (G, P, LE) herbaria were examined, as well as available online type collections of other herbaria. Protologues of all names treated were examined. Norton (1899) published several new species and varieties of *Euphorbia* from North America, and although he cited several syntypes for these names, he usually made annotations of "types" on particular herbarium sheets. Such specimens are designated here as lectotypes. In other cases, if several duplicates of the type collection were located, the holotype was assumed to come from the herbarium where the author of the name was working at the time (e.g., MO for G. Engelmann, RM for A. Nelson, and F for C. Millspaugh).

Native species in the FNA area are arranged alphabetically. For every accepted name or synonym recognized, typification information is provided. Relationships of North American species or species groups to Eurasian groups are discussed initially and in the individual species listings.

RESULTS

The 17 native species of *Euphorbia* subgenus *Esula* represent a number of different lineages, based on morphological and molecular data, and they can be separated into the five main groups listed below. Since molecular phylogenetic data for the subgenus is still preliminary and broader taxon sampling is in progress, we focus our discussion here on current morphological concepts of sections, which we acknowledge are likely to be superseded once more molecular data is obtained and analyzed. Our main reference is to the infrageneric system developed by Geltman (2007), which covers all the temperate Eurasian species of *Euphorbia*.

1. *Euphorbia purpurea* (Raf.) Fernald.—this species is unique among the North American esuloid Euphorbias, since it is a perennial, shady forest-edge species with warty fruits, and it has an eastern Appalachian/Alleghenian distribution. In the Geltman (2007, 2008) system, it belongs to *E.* sect. *Chamaebuxus* Lazaro, which consists of about 95 perennial species that have hornless, elliptical cyathial glands, usually warty fruits, and shiny brown seeds. With the exception of *E. purpurea*, all other members of the section are native to the Old World, occurring in Eurasia or Mediterranean North Africa, from the Atlantic Ocean across the continent to the Pacific, and with a few species extending into the mountains of east tropical Africa. Two European species that may be closely allied to *E. purpurea* are *E. hyberna* L. (Spain, France, Italy, and the British Isles) and *E. squamosa* Willd. (Caucasus region), both of which also occur in broadleaf forests.

2. *Euphorbia trichotoma* Kunth.—this species is also unique among the North American esuloid Euphorbias, because it is a subtropical Caribbean maritime perennial species, occurring along beaches in southern Florida. It is similar in habit to the maritime *E. paralias* L., which is native to the Atlantic and Mediterranean shores of Europe, and molecular data (Geltman et al. 2010; Kryukov et al. 2010) place it close to this species, which belongs to *E.* sect. *Paralias* Dumort. subsect. *Paraliodieae* Prokh.

3. *Euphorbia brachycera* group.—this is a group of five species that occur mainly in the western U.S. and are perennials with short-horned or irregularly dentate cyathial glands and irregularly and shallowly pitted to nearly smooth seeds. Based on these characters, they are morphologically most closely allied with the Eurasian *E.* sect. *Herpetorrhiza* (Prokh.) Prokh., which comprises about 15 species from Central Asia and the Mediterranean region. Besides *E. brachycera* Engelm., the group includes *E. chamaesula* Boiss., *E. lurida* Engelm., *E. schizoloba* Engelm., and *E. yaquiana* Tidestr.

4. *Euphorbia commutata* group.—this is a group of seven annual species with horned glands, smooth fruits, and diversely ornamented (or rarely smooth) seeds. In the Eurasian classification system, they belong to *E.* sect. *Peplus* Lázaro, which consists of seven subsections that are probably paraphyletic, based on initial molecular data (Kryukov et al. 2010). Besides *E. commutata* Engelm., the group includes *E. crenulata* Engelm., *E. helleri* Millsp., *E. longicruris* Scheele, *E. peplidion* Engelm., *E. roemeriana* Scheele, and *E. tetrapora* Engelm.

Despite being an annual, *E. crenulata* may in fact be more closely related to members of the *E. brachycera* group, based on similarities in seed and leaf morphology with *E. lurida*. Molecular studies underway will hopefully better resolve this issue. In addition to the seven species listed here, there appear to be two undescribed annual species in this group from the United States, one a very small-statured species from the sand sheet area of southernmost Texas, and the other a relative of *E. commutata* from Arkansas, Kansas, Missouri, and Oklahoma (M. Mayfield, pers. comm.).

5. *Euphorbia spathulata* group.—this is a group of three closely related, mainly annual species that have hornless cyathial glands and usually warty fruits. However, some members of this group, which belongs to *E.* sect. *Helioscopia* Dumort., have apparently reverted to smooth-surfaced fruits. Besides *E. spathulata* Lam., the group includes *E. alta* Norton and *E. texana* Boiss. *Euphorbia spathulata* is one of the most widespread native species of *Euphorbia* in the New World, occurring in most states in the U.S., as well as in Canada and Mexico.

TAXONOMIC TREATMENT

1. Euphorbia alta Norton, N. Amer. Euphorbia 24, pl. 24. 1899. *Tithymalus altus* (Norton) Wooton & Standl., Contr. U.S. Natl. Herb. 16:145. 1913. Type: U.S.A. Arizona [Cochise Co.]: Huachuca Mountains, 3 Jul 1884, *C.G. Pringle s.n.* (lectotype, designated by Steinmann & Felger 1997:51: US 19636!; duplicates of lectotype: GH!, MICH!, MO!, MPU!, US 798481!).

This is a montane species from southern Arizona, New Mexico, and northern to central Mexico. It is part of the *E. spathulata* group. It is very similar to *E. spathulata* and frequently confused with it, but the ovaries and capsules of *E. alta* are distinctly papillate, with the papillae rising sharply above the surface, whereas in *E. spathulata* the ovaries and capsules are merely verrucose, with the protuberances lower and rounder (Steinmann & Felger 1997). Also, *E. alta* is usually a more robust and taller plant than *E. spathulata,* and it has been described as a biennial or a perennial, whereas *E. spathulata* is strictly annual.

2. Euphorbia brachycera Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858. *Tithymalus brachycerus* (Engelm.) Small, Fl. S.E. U.S., ed. 2:1349. 1913. Type: U.S.A. [New Mexico. Dona Ana Co.]: "N. Mex., Donana, above El Paso," 1851, *C. Wright 1821* (holotype: MO 149763!; isotypes: GH!, NY!, P!).

Tithymalus fendleri Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859:85. 1860. Type: U.S.A. new mexico: Plantae Novo-Mexicanae, on Santa Fe Creek and the base and declivities of the mountains, May–Jul 1847, *A. Fendler 786* (holotype: B, destroyed; isotypes: MO 149776!, NY 263148!).

Euphorbia robusta (Engelm.) Small in N.L. Britton & A. Brown, Ill. Fl. N. U.S. 2:381. 1897. *Euphorbia montana* var. *robusta* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858, nom. illeg. *Tithymalus robustus* (Engelm.) Small in N.L. Britton & A. Brown, Ill. Fl. N. U.S., ed. 2, 2:475. 1913. *Galarhoeus robustus* (Engelm.) Rydb., Brittonia 1:93. 1931. *Euphorbia brachycera* var. *robusta* (Engelm.) Dorn, Vasc. Pl. Wyoming 296. 1988. Type: U.S.A.: "Frémont's expedition to the Rocky Mountains, on the upper Platte," 1842, *J.C. Frémont s.n.* (lectotype, designated here: NY 263150!). Three syntypes (*Frémont s.n.*, *James s.n.*, and *Nuttall s.n.*) were listed by Engelmann, but none of these were found at MO, consistent with the findings of Wolf (1988). The Frémont and the James collections are at NY, and we chose the better specimen of Fremont as lectotype.

Euphorbia robusta var. *interioris* Norton, N. Amer. Euphorbia 49, pl. 49. 1899. Type: U.S.A. Utah: Wasatch Mts., 9 Jun 1869, *S. Watson 1081* (lectotype, designated here, Norton, in herb.: US 19574!; duplicates of lectotype: GH!, NY!).

Tithymalus philorus Cockerell, Muhlenbergia 4:56. 1908. *Euphorbia montana* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858, nom. illeg., non Raf., Amer. Monthly Mag. & Crit. Rev. 1(6):440. 1817. *Euphorbia montana* var. *gracilior* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858, nom. illeg. *Euphorbia philora* (Cockerell) Tidestr., Proc. Biol. Soc. Wash. 48:41. 1935. Type: U.S.A. New Mexico: Plantae Novo-Mexicanae, on Santa Fe Creek and the base and declivities of the mountains, May-Jul 1847, *A. Fendler 786* (lectotype, designated by Norton 1899:44: MO 149776!; duplicate of lectotype: NY 263148!).

Tithymalus philorus f. *dichotomus* Daniels, Univ. Missouri Stud., Sci. Ser. 2:165. 1911. *Euphorbia brachycera* f. *dichotoma* (Daniels) Oudejans, Collect. Bot. (Barcelona) 21:184. 1992 publ. 1993. Type: U.S.A. Colorado: from the high ridges of Green Mt., *F.P. Daniels 367* (holotype: COLO).

This is a widespread, western North America perennial species known from Arizona, Colorado, Idaho, Montana, Nebraska, New Mexico, Nevada, North Dakota, South Dakota, Texas, Utah, and Wyoming, extending also into northern Mexico. It belongs to the *E. brachycera* species group. *Euphorbia brachycera* as delimited here constitutes a variable taxonomic complex that has sometimes been split into two or more species. When recognized as a distinct species, *E. robusta* is a more robust, low-growing, generally northern entity from Arizona, Colorado, Idaho, Montana, Nebraska, South Dakota, Utah, and Wyoming.

3. Euphorbia chamaesula Boiss., Cent. Euphorb. 38. 1860. *Tithymalus chamaesula* (Boiss.) Wooton & Standl., Contr. U.S. Natl. Herb. 16:145. 1913. Type: U.S.A. [New Mexico]: "N. Mex., 1851–52," *C. Wright 1820* (holotype: G!; isotypes: F [fragment ex G]!, GH!, MO!, NY!, US!).

Euphorbia esuliformis var. *subdentata* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858. *Euphorbia chamaesula* var. *subdentata* (Engelm.) Norton, N. Amer. Euphorbia 47, pl. 47. 1899. Type: U.S.A. [probably Arizona. Coconino Co.]: San Francisco Spring, Mar 1852, *C.C. Parry s.n.* (holotype: MO 149764!).

This is a perennial species from Arizona, New Mexico, and northern Mexico that belongs to the *E. brachycera* group of western U.S. perennials. Plants are usually taller than other species in the group, with longer leaves and larger fruits and seeds.

4. Euphorbia commutata Engelm. ex A. Gray, Manual, ed. 2:389. 1856. *Tithymalus commutatus* (Engelm. ex A.Gray) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859. 82. 1860. *Galarhoeus commutatus* (Engelm. ex A.Gray) Small ex Rydb., Fl. Plains N. Amer. 520. 1932. Type: U.S.A. Missouri: In Herculaneum … Gasconade, May 1835, *[G. Engelmann] 82* (lectotype, designated here: MO 1910962!). No specimens were cited by Gray in the protologue, but Engelmann annotated his own specimen at MO as this species (Wolf 1988).

Euphorbia ohiotica Steud. & Hochst. ex Boiss. in A.P. de Candolle, Prodr. 15(2):142. 1862. Type: U.S.A. [South Carolina]: in silvis montanis Carolina sept., May 1841, *F. Rügel s.n.* (lectotype, designated here: G!).

Euphorbia commutata var. *erecta* Norton, N. Amer. Euphorbia 35. 1899. *Tithymalus commutatus* var. *erectus* (Norton) Small, Fl. S.E. U.S. 720. 1903. *Galarhoeus commutatus* var. *erectus* (Norton) Small, Man. S.E. Fl. 801. 1933. Type: U.S.A. Florida: Hibernia, Mar 1869, *W.M. Canby s.n.* (lectotype, designated here: GH!: duplicates of lectotype: MO!, NY!).

This is an annual (or occasionally reported as a perennial) species in the *E. commutata* species group and occurs from the eastern U.S. (from Florida north to Pennsylvania), west to Illinois, Iowa, Missouri, Oklahoma, and Texas, and north to Ontario, Canada. *Tithymalus austrinus* Small should be excluded from the synonymy of *E. commutata* (listed as such by Govaerts et al. 2000). Study of the type specimen shows that it belongs to the introduced European species *E. segetalis* L.

5. Euphorbia crenulata Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):192. 1858. *Euphorbia leptocera* var. *crenulata* (Engelm.) Boiss. in A.P. de Candolle, Prodr. 15(2):143. 1862. *Tithymalus crenulatus* (Engelm.) A. Heller, Muhlenbergia 1:55. 1904. Type: U.S.A. California. Monterey Co.: Monterey, 1850, *C.C. Parry s.n.* (lectotype, designated here: NY 263094!). Engelmann cited two syntypes, *Hartweg 1950,* and *Parry s.n.* from Monterey. Neither one of these is at MO, although an empty packet taken from the GH specimen of *Hartweg 1950* was mentioned by Wolf (1988).

Euphorbia leptocera Engelm. ex Boiss. in A.P. de Candolle, Prodr. 15(2):143. 1862. *Tithymalus leptocerus* (Engelm. ex Boiss.) Arthur, Torreya 22:30. 1922. Type: U.S.A. California. [Sonoma Co.]: Colonia Ross, 1833, *F.P. Wrangel s.n.* (lectotype, designated here: LE!).

Euphorbia crenulata var. *franciscana* Norton, N. Amer. Euphorbia 38. 1899. *Tithymalus franciscanus* (Norton) A. Heller, Muhlenbergia 1:56. 1904. Type: U.S.A. CALIFORNIA [San Francisco Co.]: San Francisco, Mission hills, on cultivated fields, May 1865, *H. Bolander 20* (lectotype, designated here, Norton in herb.: MO 1910115!).

Euphorbia manca A. Nelson, Bot. Gaz. 47:437. 1909. *Tithymalus mancus* (A. Nelson) A. Heller, Muhlenbergia 9:67. 1913. Type: U.S.A. Colorado: southern Colorado, Mancos, common about edges of thickets along river bottom, 23 Jun 1898, *C.F. Baker, F.S. Earle & S.M. Tracy 23* (holotype: RM!; isotypes: GH!, NY!, US!).

Euphorbia nortoniana A. Nelson, Bot. Gaz. 47:437. 1909. Type: U.S.A. California: sand hills near the Marine Hospital, San Francisco, 25 Apr 1903, *A.A. Heller 6625* (lectotype, designated here: RM!; duplicates of lectotype: GH!, LE!, MO!, NY!, PH!, US!).

This is an annual species in the *E. commutata* species group that is widespread in California and Oregon and also occurs in Arizona and southwestern Colorado.

6. Euphorbia helleri Millsp., Bot. Gaz. 26:268. 1898. *Tithymalus helleri* (Millsp.) Small, Fl. S.E. U.S. 719. 1903. Type: U.S.A. Texas: southern Texas, ad Corpus Christi, Nueces County, 23–30 Mar 1894, *A.A. Heller 1509* (holotype: F 196474!; isotypes: GH!, MICH!, MSC, NY!, US!).

This is an annual species in the *E. commutata* group and occurs in Louisiana, Texas, and northern Mexico (Nuevo León).

7. Euphorbia longicruris Scheele, Linnaea 22:152. 1849. *Tithymalus longicruris* (Scheele) Small, Fl. S.E. U.S. 719. 1903. Type: U.S.A. Texas. [Comal Co.]: "bei Neu-Braunfels [New Braunfels]…," 16 Apr 1846, *F. Lindheimer 529 (90a)* (neotype, designated here: MO 1911068!; isoneotype: LE!).

Euphorbia peploides Nutt., Trans. Amer. Philos. Soc., n.s., 5:172. 1835, nom. illeg., non Gouan, Fl. Monsp. 174. 1764.

This is an annual species in the *E. commutata* group that occurs in Arkansas, Texas, Oklahoma, and northern Mexico (Nuevo León). Scheele's protologue cited a C.F. Roemer collection from New Braunfels as the type, but we were unable to locate any Roemer collection associated with this name. Since Ferdinand Lindheimer collected in the same area with Roemer (Goyne 1991), and many of Scheele's new species were based on Lindheimer collections as well as on Roemer's, we chose one of Lindheimer's collections from the type locality as the neotype.

8. Euphorbia lurida Engelm., Proc. Amer. Acad. Arts 5:173. 1861. *Tithymalus luridus* (Engelm.) Wooton & Standl., Contr. U.S. Natl. Herb. 16:145. 1913. Type: U.S.A. Arizona: Camps 81–82 near Leroux's Spring, foot of Bill Williams Mtn., 7000–8000 ft, 27 Apr 1858, *J.S. Newberry s.n.* (holotype: MO 149770!, isotype: GH!).

Euphorbia palmeri Engelm. ex S. Watson, Bot. California 2:75. 1880. *Tithymalus palmeri* (Engelm. ex S. Watson) Dayton, Misc. Publ. U.S. Dept. Agric. 101:93. 1931. Type: U.S.A. CALIFORNIA [San Diego Co.]: Talley's Ranch in the Cuyamaca Mountains, Jul 1875, *E. Palmer 450* (holotype: GH!, isotypes: F!, MO 149780!, NY!, PH!).

Euphorbia subpubens Engelm. ex S. Watson, Bot. California 2:76. 1880. *Tithymalus subpubens* (Engelm.) Norton, Contr. U.S. Natl. Herb. 35:342. 1925. *E. palmeri* var. *subpubens* (Engelm.) L.C. Wheeler, J. Wash. Acad. Sci. 30:473. 1940. Type: U.S.A. Arizona: Prescott Mt., 20 Apr 1876, *E. Palmer 512* (lectotype, designated here: GH 47742!; duplicates of lectotype: MO 149784!, MO 149785! –with sketch by S. Watson, NY!).

Euphorbia palmeri var. *peplofolia* Norton, N. Amer. Euphorbia 41. 1899. *Euphorbia peplofolia* Engelm. ex Patt., Checklist N. Amer. Pl. 114. 1887, nom. nud. Type: U.S.A. "Southern Utah, Arizona &c, 1877," *E. Palmer 440* (lectotype, designated here, Norton in herb.: MO 149781!).

Euphorbia lurida var. *pringlei* Norton, N. Amer. Euphorbia 39. 1899. Type: U.S.A. Arizona: Santa Rita Mountains, 5500 ft, 2 May 1881, *C.G. Pringle s.n.* (lectotype, designated here, Wheeler in herb.: MO 149771!; duplicates of lectotype: MICH!, MO 202563!, NY!, US!).

This is a western U. S. perennial species known from Arizona, California, New Mexico, Nevada, and northern Mexico. It belongs to the *E. brachycera* species group.

9. Euphorbia peplidion Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):191. 1858. *Tithymalus peplidion* (Engelm.) Small, Fl. S.E. U.S. 720. 1903. Type: U.S.A. Texas [Val Verde Co.]: stony prairies east of San Pedro, [21–22 May] 1851, *C. Wright 1823* (holotype: MO 1911115!; isotypes: G!, GH!, NY!, P!, US!).

This is an annual species endemic to south-central and western Texas that belongs to *E. commutata* group and is very similar in seed characters to the European *E. peplus* L.

10. Euphorbia purpurea (Raf.) Fernald, Rhodora 34:25. 1932. *Agaloma purpurea* Raf., Autik. Bot. 94. 1840. Type: U.S.A. Pennsylvania: shaded rivulet on the Barrens above S. Stringfellow's, West Chester, 11 Jul 1819, *W. Darlington s.n.* (neotype, designated here: PH 01070036!).

Euphorbia darlingtonii A. Gray, Manual 404. 1848. *Euphorbia nemoralis* Darl., Fl. Cestr., ed. 2, 518. 1837, nom. illeg., non Salisb., Prodr. Stirp. Chap. Allerton 390. 1796. *Tithymalus darlingtonii* (A. Gray) Small, Fl. S.E. U.S. 719. 1903. *Galarhoeus darlingtonii* (A. Gray) Small, Man. S.E. Fl. 801. 1933. Type: U.S.A. PENNSYLVANIA: shaded rivulet on the Barrens above S. Stringfellow's, West Chester, 11 Jul 1819, *W. Darlington s.n.* (lectotype, designated here: PH 01070036!).

Euphorbia darlingtonii var. *glabra* Boiss. in A.P. de Candolle, Prodr. 15(2):119. 1862. Type: U.S.A. [North Carolina]: in montibus Blue Ridge, Aug 1841, *F. Rügel s.n.* (holotype: G!).

We found no original Rafinesque type material of *Agaloma purpurea* (DTW and P were checked carefully), so Darlington's collection from the same area was chosen as the neotype. *Euphorbia purpurea* is a distinctive forest-inhabiting perennial species that is native to the Appalachian and Allegheny Mountains and adjacent areas in Delaware, Maryland, New Jersey, North Carolina, Ohio, Pennsylvania, Virginia, and West Virginia. It is more closely allied to other European members of *E.* sect. *Chamaebuxus* than it is to any other native North American species. This is likely why Willdenow (1799) originally identified it as *E. pilosa* L., a warty-fruited Eurasian perennial. Pursh (1814) also treated the American material as *E. pilosa* and referred back to the same Willdenow publication. For unexplained reasons, Norton (1899) treated Pursh's citation as a new species, *E. pilosa* Pursh (not Willd.), and listed it as a synonym of *E. darlingtonii* (= *E. purpurea*). However, it was clearly not Pursh's intention to treat this as a new species, and he was just following Willdenow's use of the name. Govaerts et al. (2000) treated *Keraselma ciliata* Raf. as a synonym of *E. purpurea*, but Rafinesque

(1840) stated that *K. ciliata* is an annual that occurs in Missouri, so it clearly cannot be the same species as *E. purpurea*. We have not seen any original material of *K. ciliata* and therefore cannot place it with confidence, but we suspect it would most likely correspond to either *E. commutata* or *E. spathulata*.

11. Euphorbia roemeriana Scheele, Linnaea 22:151. 1849. *Tithymalus roemerianus* (Scheele) Small, Fl. S.E. U.S. 720. 1903. Type: U.S.A. Texas [Comal Co.]: [New Braunfels], Apr 1846, *F. Lindheimer 528 (89)* (neotype, designated here: MO 1911159!; isoneotype: LE!).

This is an annual species in the *E. commutata* species group that is endemic to central Texas. As with *E. longicruris,* we were unable to locate any collection of C.F. Roemer corresponding to this name, so we are using a Lindheimer collection gathered in the same area and possibly together with Roemer (Goyne 1991) as the neotype.

12. Euphorbia schizoloba Engelm., Proc. Amer. Acad. Arts 5:173. 1861. *Tithymalus schizolobus* (Engelm.) Norton, Contr. U.S. Natl. Herb. 25:343. 1925. Type: U.S.A. Arizona: Camp 62, Central Range, in eastern Arizona, east of Colorado river, Railroad Pass, 3346 ft, 26 Mar 1858, *J.S. Newberry s.n.* (holotype: MO 144648!; isotypes: G!, GH 27738 –specimen on the left!, NY 263179!).

Euphorbia incisa Engelm. in Ives, Rep. Colorado R. 4:27. 1861. *Tithymalus incisus* (Engelm.) W.A. Weber, Phytologia 67:428. 1989. Type: U.S.A. Arizona: Camp 62, Central Range, in eastern Arizona, east of Colorado river, Railroad Pass, 3346 ft, 26 Mar 1858, *J.S. Newberry s.n.* (holotype: MO 144648!; isotypes: G!, GH 277308 –specimen on the left!, NY 263179!).

Euphorbia odontadenia Boiss. in A.P. de Candolle, Prodr. 15(2):148. 1862. Type: U.S.A. [New Mexico]: mountains, El Paso, "N. Mex." 1851–52, *C. Wright 1825* (holotype: G!; isotypes: GH!, MO!).

This is a perennial species in the *Euphorbia brachycera* group that is endemic to Arizona, California, Nevada, and New Mexico. Engelmann published two different names for this species in the same year (*E. incisa* and *E. schizoloba*). Although we have not been able to determine which publication has priority, Engelmann himself cited *E. incisa* as a synonym of *E. schizoloba* (in Watson, 1880), as did Norton (1899). Also, the type specimen at MO was annotated by Engelmann as *E. schizoloba*, and there is no mention of the name *E. incisa* on the sheet.

Some authors have included *E. odontadenia* as a synonym of *E. brachycera* (e.g., Norton 1899). Kearney and Peebles (1951), however, recognized *E. odontadenia* as an uncertain entity that was closely allied to *E. schizoloba* (as *E. incisa*). Our examination of the type material places it here under *E. schizoloba*.

13. Euphorbia spathulata Lam., Encycl. 2:428. 1788. *Keraselma spathulata* (Lam.) Raf., Autik. Bot. 93. 1840. *Tithymalus spathulatus* (Lam.) W.A. Weber, Phytologia 58:384. 1985. Type: URUGUAY: near Montevideo, *P. Commerson s.n.* (holotype: P-LAM; isotype: MPU!).

Euphorbia obtusata Pursh, Fl. Amer. Sept. 2:606. 1814. *Pythius obtusata* (Pursh) Raf., Fl. Tellur. 4:116. 1838. *Tithymalus obtusatus* (Pursh) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859:69. 1860. *Galarhoeus obtusatus* (Pursh) Small ex Rydb., Fl. Plains N. Amer. 520. 1932. Type: U.S.A. Virginia: Staunton, 1806, *F.T. Pursh 116* (lectotype, designated here: PH 01021023!, fragment on far right of sheet). The lectotype is on a sheet with three different collections of the same species, and the Pursh collection is annotated as the "type specimen" of "*Euphorbia obtusata* Fl. Amer."

Euphorbia dictyosperma Fisch. & C.A. Mey., Index Seminum (LE) 2:37. 1836. *Tithymalus dictyospermus* (Fisch. & C.A. Mey.) A. Heller, Muhlenbergia 1:56. 1904. PROTOLOGUE: "In portu Bodega Novae Californiae." Type: U.S.A. California: "California, cult. in h.b. Petrop., 1835," *C.A. Meyer s.n.* (lectotype, designated here: LE!). There were no specimens cited in the protologue, and there are several collections at LE labeled *E. dictyosperma* that had been grown at the botanical garden in Saint Petersburg and could have been used by the authors to make their description. We chose as lectotype a specimen made by Meyer himself.

Xamesike deltifolia Raf., Autik. Bot. 98. 1840. PROTOLOGUE: "Florida." Type: reported by Merrill (1949) to be a Rafinesque collection at P from the Durand Herbarium, but not found before P was closed for renovations in 2010.

Euphorbia arkansana Engelm. & A. Gray, Boston J. Nat. Hist. 5 (Pl. Lindheim.):261. 1845. *Tithymalus arkansanus* (Engelm. & A.Gray) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859:66. 1860. *Galarhoeus arkansanus* (Engelm. & A. Gray) Small ex Rydb., Fl. Plains N. Amer. 520. 1932. Type: U.S.A. Texas: near Houston, Comal Spring, Jun 1845, *F. Lindheimer s.n. [Flora Texana exsicatta 302]* (lectotype, designated here: MO 1910040!; duplicates of lectotype: GH!, LE!, NY!).

Euphorbia dictyosperma var. *mexicana* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):191. 1858. *Euphorbia mexicana* (Engelm.) Norton, N. Amer. Euphorbia 21, pl. 21. 1899. *Tithymalus mexicanus* (Engelm.) Wooton & Standl., Contr. U.S. Natl. Herb. 16:145. 1913. *Euphorbia spathulata* var. *mexicana* (Engelm.) Oudejans, Collect. Bot. (Barcelona) 21:188. 1992 publ. 1993. Type: MEXICO [Durango]: Bolsón de Mapimí, Valley of Nazas, 15 Apr 1847, *J. Gregg 456* (lectotype, designated by Wolf 1988:1626: MO 149772!).

Euphorbia dictyosperma var. *multicaulis* J.M. Coult., Contr. U.S. Natl. Herb. 2:393. 1894. *Euphorbia multicaulis* Engelm. in W.H. Emory,

Rep. U.S. Mex. Bound. 2(1):191. 1858, nom. illeg. Type: MEXICO. Sonora: Los Playos [Las Playas?], May 1851, *G. Thurber 381* (holotype: MO 149774!).

Euphorbia arkansana var. *atrosemina* Norton, N. Amer. Euphorbia 21, pl. 20. 1899. Type: U.S.A. Arizona: foothills of the Santa Rita Mountains, 19 May 1894, *C.G. Pringle s.n.* (lectotype, designated here, Norton in herb.: US 19649!; duplicate of lectotype: GH!).

Euphorbia arkansana var. *coloradensis* Norton, N. Amer. Euphorbia 21, pl. 19. 1899. *Tithymalus arkansanus* var. *coloradensis* (Norton) Rydb., Bull. Torrey Bot. Club 33:145. 1906. Type: U.S.A. Colorado: Clear Creek Cañon, 20 Jun 1878, *M.E. Jones 239* (lectotype, designated here, Norton in herb.: MO 1910062!).

Euphorbia arkansana var. *missouriensis* Norton, N. Amer. Euphorbia 19, pl. 18. 1899. *Euphorbia missouriensis* (Norton) Small in N.L. Britton, Man. Fl. N. States 595. 1901. *Tithymalus missouriensis* (Norton) Small, Fl. S.E. U.S. 721. 1903. *Galarhoeus missouriensis* (Norton) Rydb., Brittonia 1:93. 1931. Type: U.S.A. KANSAS. Manhattan, 11 Jun 1897, *J.B.S. Norton s.n.* (lectotype, designated here, Norton in herb.: MO!).

Euphorbia pseudopeplus Speg., Anales Mus. Nac. Buenos Aires 7:164. 1902. *Tithymalus pseudopeplus* (Speg.) Soják, Cas. Nár. Mus., Odd. Prír. 148:199. 1979 publ. 1980. Type: ARGENTINA. [Rio Negro. Dpto. Adolfo Alsina]: prope Carmen de Patagones, Feb 1898," *C. Spegazzini (Herbarium Spegazzini 12560)* (lectotype, designated here: LP).

This is the most widespread species of *Euphorbia* subg. *Esula* in the New World. It is an annual species in the *E. spathulata* species group that is known from Ontario, Canada, northern Mexico, and most states in the U.S., except for Nevada and the northeastern states. It also occurs disjunctly in Argentina, Uruguay, and southern Brazil, where it is considered to be adventive (Correa 1988). So far, we have not been able to locate the holotype specimen at P.

14. Euphorbia tetrapora Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):191. 1858. *Tithymalus tetraporus* (Engelm.) Small, Fl. S.E. U.S. 720. 1903. Type: U.S.A. [Louisiana]: "Red River, Louisiana," *J. Hale s.n.* (lectotype, designated here: MO 191173!).

Euphorbia tetrapora var. *berlandieri* Boiss. in A.P. de Candolle, Prodr. 15(2):142. 1862. Type: U.S.A. Texas: de Bejar ad Rio de la Trinidad, May 1828, *J.L. Berlandier 1664* (holotype: G!; isotype: P 00716338!).

This is an annual species endemic to Texas, Oklahoma, and Louisiana that belongs to the *E. commutata* group.

15. Euphorbia texana Boiss., Cent. Euphorb. 30. 1860. Type: U.S.A. TEXAS: Texas, 1835, *T. Drummond 327* (holotype: LE [ex Herb. Hooker]!; isotypes: GH!, LE [ex Herb. Fischer]!, MO!, NY!).

Euphorbia dictyosperma var. *leiococca* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):191. 1858. *Euphorbia leiococca* (Engelm.) Norton, N. Amer. Euphorbia 24, pl. 25. 1899. *Tithymalus leiococcus* (Engelm.) Small, Fl. S.E. U.S. 721. 1903. Type: U.S.A. Texas: Texas, 1835, *T. Drummond 327* (lectotype, designated by Wolf 1988:1626: MO 1911059!; duplicates of lectotype: GH!, LE [2 sheets]!, NY!).

This is a small annual species endemic to Texas that belongs to *E. spathulata* group, but it differs from *E. alta* and *E. spathulata* in its smooth fruits. This character is also found in the European *E. helioscopia* L.

16. Euphorbia trichotoma Kunth in F.W.H. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 2:60. 1817. *Tithymalus trichotomus* (Kunth) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859:81. 1860. *Galarhoeus trichotomus* (Kunth) Small, Man. S.E. Fl. 802. 1933. Type: CUBA: Havana, in maritimis, May 1801, *A. von Humboldt & A. Bonpland 1415* (holotype: P-BONP!; isotype: P 00136065!).

Euphorbia dumosa A. Rich. in R. de la Sagra, Hist. Fis. Cuba, Bot. 11:2:198. 1850. PROTOLOGUE: "In ruderatis et maritimis Insulae Cubae." Type: (P – not seen).

Euphorbia trichotoma var. *macilenta* Millsp., Publ. Field Columb. Mus., Bot. Ser. 2:67. 1900. Type: MEXICO. Quintana Roo: Cozumel Isl., East Shore, 21 Feb 1899, *C.F. Millspaugh 1598* (lectotype, designated here: F 196878!).

This is a Caribbean maritime species known only from southern Florida in the FNA area. It is unlike any other North American native species and is related to *E. paralias* L. from Atlantic and Mediterranean shorelines of Europe. Since the herbarium at P has been closed for extensive renovations, we were not able to search for the type of *E. dumosa* there.

17. Euphorbia yaquiana Tidestr., Proc. Biol. Soc. Wash. 48:41. 1935. *Euphorbia mollis* Engelm. ex Patt., Checklist N. Amer. Pl. 114. 1887, nom. nud. *Euphorbia schizoloba* var. *mollis* Norton, N. Amer. Euphorbia 43, pl. 43. 1899. *Euphorbia incisa* var. *mollis* (Norton) L.C. Wheeler, J. Wash. Acad. Sci. 30:473. 1940. Type: U.S.A. Arizona: Canyons, Santa Catalina Mts., 19 Apr 1881, *C.G. Pringle s.n.* (lectotype, designated here: MO 149782!; DUPLICATES OF LECTOTYPE: GH!, NY [4 sheets]!, P!).

This is a perennial species in the *E. brachycera* species group that is endemic to Arizona.

ACKNOWLEDGMENTS

The work was supported by a joint grant of the U.S. Civil Research and Development Foundation (project N RUB1-2916-ST-07) and the Russian Foundation for Basic Research (project N 08-04-91103), as well as a NSF Planetary Biodiversity Inventory award (DEB 0616533). We are grateful to the curators of herbaria (DWC, G, GH, KSC, LE, NY, MICH, MO, P, RM, US) for allowing us to examine their holdings, and to Sharon Bartholomew-Began for providing photographs of the historic Euphorbiaceae specimens at DWC, Roger Kiger for his expertise on Rafinesque handwriting, and Mark Mayfield for discussions on the North American euphorbias. Victor W. Steeinmann and an anonymous reviewer provided helpful reviews.

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BOOK REVIEWS

Gregory P. Cheplick and Stanley H. Faeth. 2009. **Ecology and Evolution of the Grass-Endophyte Symbiosis.** (ISBN 13: 978-0-19-530808-2, ISBN 10: 0195308085, hbk.), Oxford University Press, Inc, 198 Madison Avenue, New York, New York 10016, U.S.A. (**Orders:** www.oup.com/us/catalog/general/subject/LifeSciences/Ecology/?view=usa&ci=9780195308082; 800-451-7556; custserv.us@oup.com). $75.00, 256 pp., 5 halftones, 24 line illus., 6⅛" × 9¼".

For decades agricultural scientists were taught that plants growing properly consisted only of plant tissue and that microbes in plant tissue represented a threat to the plant. Key exceptions to that belief were the nitrogen-fixing bacteria associated with the roots of legumes. These associations represented mutually beneficial interactions between the host plant and the microorganisms.

With further study over time additional beneficial plant –microbe interactions were discovered and studied. Nitrogen fixation was demonstrated in plants-bacterial associations outside legumes.

Mycorrhizal fungi were shown to enhance the growth of many plants by facilitating micronutrient uptake, further expanding the list of microorganisms associated with roots that provide benefits to the host plants.

Starting about 30 years ago, scientists noted the presence of fungi growing within grass leaves and stems. The fungi did not appear to be pathogens as no detrimental effects were apparent. On the other hand, it seemed that the presence of the fungi was acting as a deterrent to insects that normally feed on the grass.

Cheplick and Faeth have compiled a thorough review of the research that has now established the clear role of mutualistic fungi that grow within plant tissues. The authors contributed greatly to the research in this field and their book covers the history of this interesting area as well as the important discoveries.

As the authors note, many plants support the growth of endophytic fungi, but the majority of the research has focused on grass and fungi from the genus *Neotyphodium*. Grass plants colonized by endophytes deter herbivores. This holds true for insect and mammalian species. In the case of insects, the feeding deterrent effects of colonization are preferred; however, when the herbivores are domestic animals such as horses and cattle, the anti-feeding effects are not desirable.

The authors point out that knowledge of the effects of endophyte colonization has been used to develop grass varieties that are "infected" and are thus inherently resistant to insects.

Recent research has greatly expanded the known range of plants and fungal species that exhibit endophytic colonization. The authors cover recent developments thoroughly and go on to discuss how these mutualistic associations may be applied in the future to provide new pathways to crops that may enhance their natural resistance to various pests.

This monograph concludes with the authors' view of future research needs in this area and the implications of the possible impact of endophytic fungi on other host plant groups.—*Richard Lankow, PhD., Aspen Bioscience LLC, Fort Worth, Texas and BRIT volunteer, Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A.*

Jan Wrede. 2010. **Trees, Shrubs, and Vines of the Texas Hill Country: A Field Guide, Second Edition.** (ISBN-13:978-1-60344-188-9, ISBN-10: 1-60344-188-3, Flexbound with flaps).Texas A&M University Press, John H. Lindsey Building, Lewis Street, 4354 TAMU, College Station, Texas 77843-4354, U.S.A. (**Orders:** http://www.tamupress.com/product/Trees-Shrubs-and-Vines-of-the-Texas-Hill-Country,1872.aspx; 1-800-826-8911; Toll Free U.S. only 979-847-8752 fax). $24.00, 272 pp., 195 color photos, map, 2 tables, 8¾" × 8½".

This welcome addition to the Texas A&M series of field guides offers much more than a compilation of photos and descriptions of regional plants. The author has included an extensive section on the natural history of the Texas Hill Country along with useful advice on using native plants in the home landscape.

As director of the Cibolo Nature Center in Boerne, Texas, Ms. Wrede has intimate knowledge of the plant communities of the Central Texas Hill Country. A very nice addition to the book is a series of descriptions of invasive plants. The author discusses the threat that invasives pose to the natural landscape and notes that some invasive plants are native to the region but have expanded well beyond their historical ranges due to the influences of humans and their domestic animals. The review of the spread and threat of Mountain Cedar (*Juniperus ashei*) is detailed and well balanced.

The descriptions of the trees, shrubs, and vines are thorough, but are arranged by plant families which may make it somewhat challenging for those who are not familiar with plant taxonomic relationships. However, that is a minor point and anyone exploring the Hill Country of Central Texas will find a great deal of useful information in this book.

The author includes several charts listing native plants, where they occur, and their characteristics. An extensive list of resources will be useful to anyone seeking additional information. The resource list includes native plant societies, extension agents, and demonstration gardens along with contact names and telephone numbers.—*Richard Lankow, PhD., Aspen Bioscience LLC, Fort Worth, Texas and BRIT volunteer, Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A.*

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IMPATIENS VEERAPAZHASII (BALSAMINACEAE), A NEW SCAPIGEROUS BALSAM FROM WAYANAD, WESTERN GHATS, INDIA

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ABSTRACT

A new species of *Impatiens* L. (Balsaminaceae) allied to *I. pandata* Barnes, is described and illustrated from the Nilgiri phytogeographical region of Western Ghats of India. Conservation attributes and ecological peculiarities are discussed.

Key Words: *Impatiens*, Balsaminaceae, new species, Wayanad, Western Ghats

RESUMEN

Se describe e ilustra una nueva especie de *Impatiens* L. (Balsaminaceae) emparentada con *I. pandata* Barnes, procedente de la región fitogeográfica Nilgiri de los Western Ghats de India. Se discuten sus atributos de conservacion y peculiaridades ecológicas.

INTRODUCTION

The genus *Impatiens* (Balsaminaceae) is diversified with more than 1000 species distributed mainly in the wet tropics and in north temperate regions (Mabberley 2008). The western part of south Asia and contiguous southeast Asian regions are the major centers of diversity and endemism. A few representatives are reported from America and Europe (Mabberley 2008). In India the genus is represented by 203 taxa mainly distributed in three major centers of diversity i.e., Western Himalayas, North East India, and the Western Ghats, each characterized by its own species group (Vivekananthan et al. 1997). In India, scapigerous *Impatiens* form a peculiar section 'Scapigerae' and are restricted to Western Ghats. So far, among the world distribution range of *Impatiens*, this section is reported only from Western Ghats-Sri Lankan phytogeographical region (Grey-Wilson 1980; Vivekananthan et al. 1997) and is endemic to Western Ghats-Sri Lanka Hotspot of Biodiversity. Except *Impatiens acaulis* Arn., which is distributed throughout the wet tropical forests of Western Ghats and Sri Lanka, all the other species have very narrow distribution patterns in various small microcenters of endemism in Western Ghats, especially in its southern part. The Wayanad district of Kerala forms a biodiversity rich area in the Nilgiri Phytogeographical region of Western Ghats. Because of rich tropical forests and suitable climatic factors at an average altitude of 1000 m asl, the area supports diverse ephemerals especially a genus such as *Impatiens*.

The Wayanad district in Kerala is unique and the entire area is along the Western Ghats with altitudes ranging from 700 m to 2100 m msl. Nineteen species of *Impatiens* were reported from the Wayanad district (Ratheesh Narayanan 2009). During our floristic exploration in the tropical evergreen forests of Wayanad, some specimens of epiphytic scapigerous *Impatiens* were collected from the Kurichiarmala-Banasura hill ranges. These scapigerous *Impatiens* were strikingly different from other species of scapigerous *Impatiens,* due to their large leafy bracts, a spurless lower sepal, and tubercled, hairy, golden yellow seeds. A careful examination revealed that the leaf, bracts, and texture of the scape, size and shape of lateral united petals, dorsal auricle and seed structure are unique and distinct from all the other described species. Subsequent detailed study, close observation, and consultation of relevant literature (Hooker 1908; Barnes 1939; Grey-Wilson 1980 & 1985; Bhaskar 1981; Bhaskar & Razi 1983; Pandurangan & Nair 1995; Vivekananthan et al. 1997; Viswanathan et al. 2003; Bhaskar 2006) have confirmed the plants are distinct from all the other described taxa. Hence, it is described and illustrated here as a new species.

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Vivekananthan et al. (1997) reported 16 species of scapigerous *Impatiens* from Western Ghats in his treatment for the flora of India. Later, Viswanathan and Manikandan (2003) and Bhaskar (2006) described two new scapigerous balsams from southern Western Ghats. Classification of the section 'scapigerae' is mainly based on the spur of the lateral sepals, lobes of lateral united petals, and auricle on the lateral united petals. Among the 18 scapigerous *Impatiens* species, four species, i.e., *I. chandrasekharanii* Chandrab., *I. neo-barnesii* Fischer, *I. acaulis* Arn. and *I. orchioides* Bedd. have 2-lobed lateral united petals. Among these, *I. chandrasekharanii* Chandrab. is a peculiar species with palmately lobed leaves. The other 14 species have 3-lobed lateral united petals. Considering the dorsal auricle on the lateral united petals, species such as *I. lawsonii* Hook., *I. denisonii* Bedd., *I. barberi* Hook., and *I. clavata* Bhaskar have a dorsal auricle of wings developing into a spur. All the others are without a prominent auricle on the lateral united petals. Size and shape of the spur on the lower sepal is also a peculiar feature among the scapigerous *Impatiens*. Among the 18 taxa, 15 have a long, narrow, curved or short spur on the lower sepal. *Impatiens pandata* Barnes, *I. neo-barnesii* Fischer, and *I. orchioides* Bedd. are devoid of spurs on the lower sepal. Among these, *I. neo-barnesii* Fischer and *I. orchioides* Bedd. have 2-lobed lateral united petals. *Impatiens pandata* is the only spurless species which has 3-lobed lateral united petals. Our specimens are related to *I. pandata* because of the spurless lower sepal and the 3-lobed lateral united petals.

Impatiens veerapazhasii Ratheesh, Sujanapal, & Meera, sp. nov. (**Figs. 1–2**). Type: INDIA. Kerala. Wayanad district: Kurichiarmala, N 11°35.769' E 75°58.787' ±1500 m, 8 Aug 2007, *M.K. Ratheesh Narayanan MSSH 1003* (holotype: MH; isotypes: CALI, MSSH).

Species ad sect. *Scapigeras* labello sine calcare, petalorum aliis trilobatis pertinet, *I. pandatae* similis in characteribus floralibus, sed bracteis magnis foliaceis, folii margine distante serratis, foliis trichomatibus pluricellularibus, scapo minuto, petali alia dorsali auricula lutea, seminibus aureis tuberculatis ab omnibus differt. Ab omnibus speciebus Impatentis scapigeris bracteis magnis foliaceis differt.

Epiphytic herbs on tree trunks, to 10 cm long, scapigerous, rhizome 7–8 mm, globose, thick with numerous root hairs. Leaves 2–4, highly variable, radical, broadly ovate or ovate-lanceolate, obliquely cordate or deeply cordate at base, rounded or obtusely acute at apex, margins distantly serrate, papillate on margins, 5–10 × 2–4 cm, glabrous and light green below, many-celled trichomes on upper surface, trichomes to 2 mm; nerves 5–7 pairs, pinkish below; petiole 2–3 cm long with pinkish stripes and spots. Inflorescence scapose, unbranched, zigzig between bracts, 4–8 cm long, glabrous or with trichomes on upper portion, 3–many flowered, racemose. Flowers white with yellow center; 1.5–2 × 2–2.5 cm, pedicel 1.5–2 cm long, glabrous; bracts strongly hairy, persistent, green, leafy, 3-lobed, broadly ovate to rounded, 1–1.5 × 0.8–1.3 cm, many celled trichomes above; lateral sepals lanceolate, ca. 3 × 2 mm, acute, slightly curved. Lower sepal ca. 5 × 4 mm, ovate, spathulate, white, spurless, glabrous; dorsal petal reniform, ca. 4 × 4 mm; lateral united petals 3-lobed, ca. 13 × 8 mm, white with yellow papillate base, white hairs on upper lobe, upper lobe 5–7 × 2–3 mm, lower lobe 1–1.2 × 0.4–0.8 cm, notch 4–6 mm, dorsal auricle small, 1–2 mm, yellow; stamens 5, short and broad, anthers cohering; ovary oblong, 5-celled; ovules many; stigma sessile, 5-lobed; capsule oblong, ca. 1 cm long, subfalcate, loculicidal dehiscent, valves 5, many seeded. Seeds tubercled, ca. 1 × 0.3 mm, oblong, golden yellow, densely hairy on both ends.

Impatiens veerapazhasii resembles *I. pandata*, *I. neo-barnesii,* and *I. orchioides* in having a spurless lower sepal, but differs in habit, nature of bract, texture of leaves, shape of lateral united petals, and texture of seeds. *Impatiens veerapazhasii* is easily distinguished from all the other species of scapigerous *Impatiens* by its large foliaceous green bracts. It has many-celled trichomes on the upper leaf surface, small yellow dorsal auricle on lateral united petals, and tubercled golden yellow seeds, densely hairy on both ends in contrast to glabrous leaves, narrowly ovate, glabrous bract, lateral united petals without a dorsal auricle and granulate seeds of *I. pandata*. *Impatiens veerapazhasii* has 3-lobed lateral united petals with a small yellow dorsal auricle in contrast to the 2-lobed lateral united petals without a dorsal auricle of *I. neo-barnesii* and *I. orchioides*. Diagnostic morphological characters of *I. veerapazhasii* and related species are provided in Table 1.

Paratypes: **INDIA. Kerala. Wayanad district:** Kurichiarmala, N 11°35.769' E 75°58.787' ± *1500 m,* 20 Aug 2008, *M.K. Ratheesh Narayanan MSSH 3013,* 18 Sep, 2009, *M.K. Ratheesh Narayanan MSSH 3043* (Herb. MSSRF, Kalpetta, Wayanad).

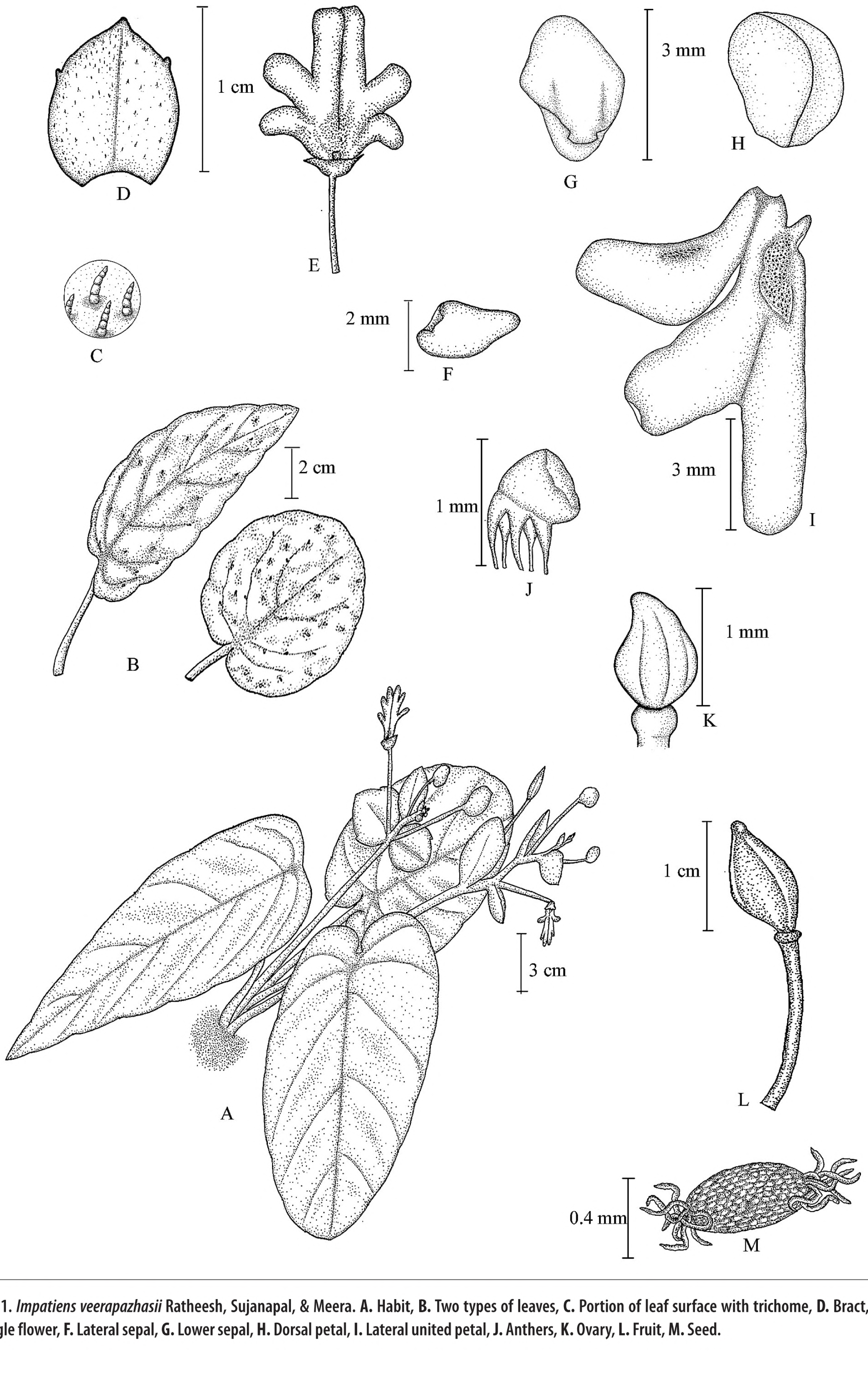

Fig. 1. ***Impatiens veerapazhasii*** **Ratheesh, Sujanapal, & Meera. A. Habit, B. Two types of leaves, C. Portion of leaf surface with trichome, D. Bract, E. Single flower, F. Lateral sepal, G. Lower sepal, H. Dorsal petal, I. Lateral united petal, J. Anthers, K. Ovary, L. Fruit, M. Seed.**

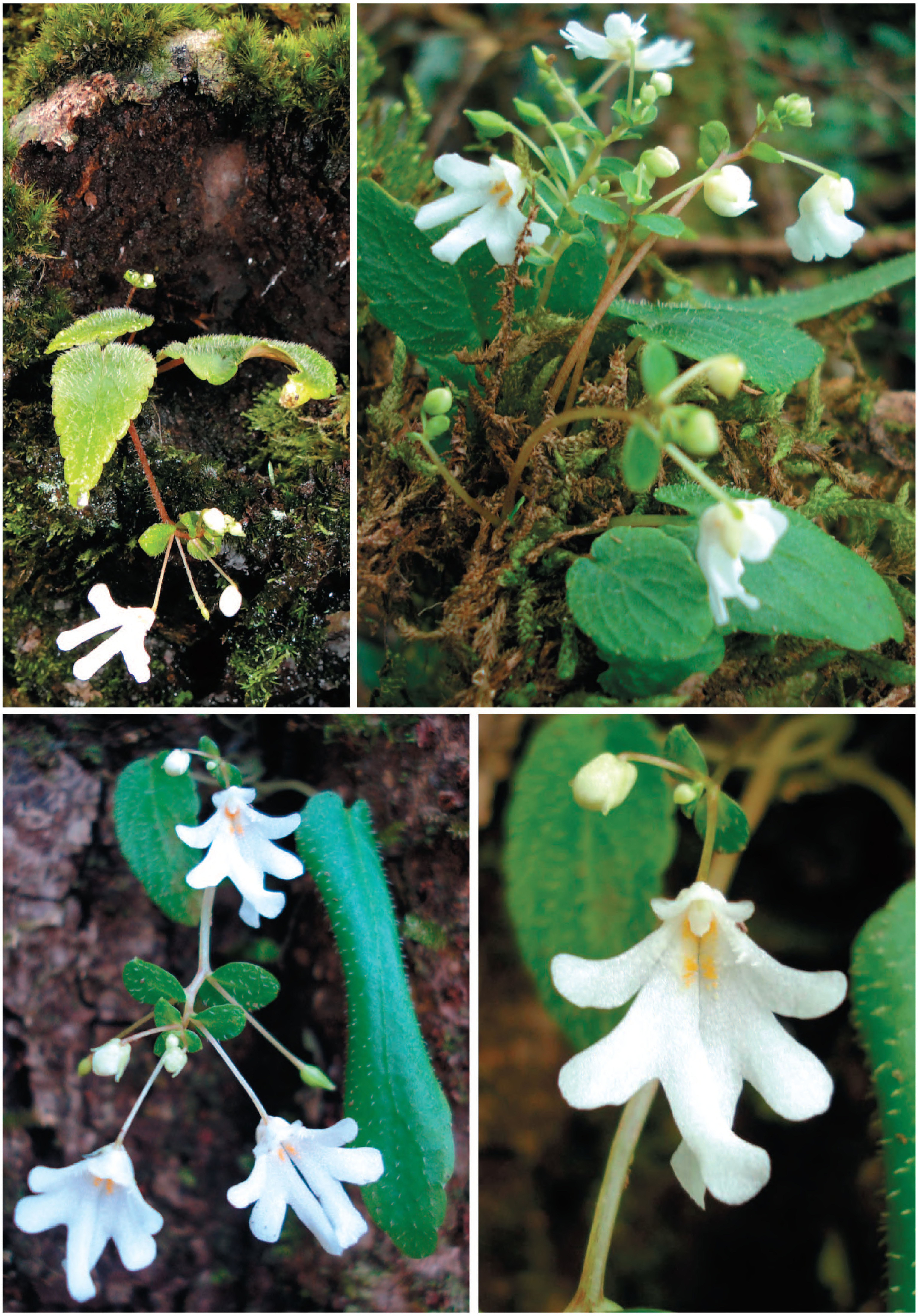

Fig. 2. *Impatiens veerapazhasii* Ratheesh, Sujanapal, & Meera. Habit and close-up of flowers.

Table 1. Diagnostic characters of *Impatiens veerapazhasii* sp. nov. and related species.

I. veerapazhasii	I. pandata	I. neo-barnesii	I. orchioides
Epiphyte on moss covered tree trunks	On wet rocks	Epiphyte on moss covered tree trunks	Epiphyte on moss covered tree trunks
Leaves ovate-lanceolate, obliquely or deeply cordate at base, distantly serrate along margins, many celled trichomes present on upper surface	Leaves orbicular-reniform, cordate at base, crenate along margin, glabrous	Leaves elliptic-ovate, base rounded, sparsely pilose above	Leaves ovate-orbicular, deeply cordate at base, crenate along margins, hairy above
Petiole 2–3 cm long	Petiole 2–3 cm long	Petiole 3–4 cm long	Petiole 2–16 cm long
Scape 4–8 cm long, 3–10-flowered, zig-zag between bracts	Scape up to 20 cm long, 9 or fewer-flowered, straight between bracts	Scape 4–5 cm long, 3–7-flowered, straight between bracts	Scape 5–19 cm long, 6–10-flowered, straight between bracts
Bract broadly ovate to rounded, green, leafy, hairy, 3 teethed	Bract narrowly ovate, glabrous	Bracts lanceolate or ovate, subacute, glabrous	Bracts ovate, glabrous
Pedicel stout, 1.5–2 cm long	Pedicel slender, up to 2.7 cm long	Pedicel 1.3–1.5 cm long	Pedicel very slender, 1–1.5 cm long
Lower sepal spathulate, spurless	Lower sepal spoon shaped, spurless	Lower sepal ovate-oblong or sub-orbicular, base shortly saccate, spurless	Lower sepal saccate, spurless
Lateral united petals 3-lobed, upper lobe smaller	Lateral united petals 3-lobed, upper curved outwards	Lateral united petals 2-lobed, upper lobe smaller	Lateral united petals 2-lobed, upper lobe pendulous, with a dimidiate oblong blade
Dorsal auricle present, 1–2 mm long, yellow	Dorsal auricle absent	Dorsal auricle absent	Dorsal auricle absent
Capsule oblong, ca. 1 cm long, subfalcate	Capsule ellipsoid, ca. 1.2 cm long	Capsule ellipsoid ca. 8 mm long	Capsule oblong ca. 1 cm long
Seeds tubercled, densely hairy on both ends	Seeds covered with white granules which swell to hairs when wet	Seeds tubercled	Seeds scrobiculate

Flowering and fruiting.—Flowering starts from July and peak time is August. Fruit matured during August–September.

Habitat.—Montane evergreen forests at an altitude of 1300–1600 m asl.

Etymology.—The specific epithet denotes the 'Lion of Kerala,' great Pazhassiraja, who made valiant movements against English rulers, fighting for freedom. Wayanad forests and its ethnic group 'Kurichya community' gave shelter and support to this great warrior, during his traditional war against the English Army.

Distribution and conservation status.—Known only from the high altitude evergreen forests in Kurichiarmala-Banasura hill ranges of Wayanad in southern Western Ghats. Small populations of this species were observed only in three locations in the area. The species is usually seen as an epiphyte on the moss covered trunk of evergreen tree species such as *Syzygium grande* (Wight) Walp. and *Calophyllum astroindicum* Kosterm. ex Stevens. This delicate species appears with the onset of monsoons and perishes within a short duration of time, even after one week of long non-rainy days in the monsoon season.

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A PHYLOGENETIC ASSESSMENT OF BREEDING SYSTEMS AND FLORAL MORPHOLOGY OF NORTH AMERICAN *IPOMOEA* (CONVOLVULACEAE)

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ABSTRACT

A phylogenetic investigation of 68 species and two varieties of tropical and temperate North American *Ipomoea* (Convolvulaceae) using sequence data from the internal transcribed spacer region (ITS) with parsimony and Bayesian analyses revealed multiple origins of autogamy. By assessing breeding systems and floral morphological characters in the context of this phylogeny, we estimate 16 independent origins of autogamy and 4 subsequent reversions to xenogamy. Transitions to autogamy are associated with reduced pollen-ovule ratios, decreased anther-stigma distance, and small flower size. Although the relationship between floral traits and breeding systems has been described in previous studies, this is the first investigation to examine this association in *Ipomoea*.

RESUMEN

Una investigación filogenética sobre 68 especies y dos variedades de *Ipomoea* (Convolvulaceae) en las zonas tropicales y templadas de Norteamérica, empleando datos de secuencias de ADN (ITS) con análisis de parsimonia y Bayesianos, demuestran orígenes múltiples de la autogamia. Basándose en la evaluación de los sistemas reproductivos y las características florales en el contexto de los resultados filogenéticos, estimamos 16 derivaciones independientes de la autogamia y cuatro reversiones a la xenogamia. Las transiciones a la autogamia se asocian con relaciones bajas de polen/óvulo, la disminución de la distancia entre las anteras y el estigma, y corolas pequeñas. Aunque estudios previos han tratado de las relaciones entre los sistemas reproductivos y los rasgos florales en las angiospermas, el presente estudio representa el primero que investigua estas relaciones en *Ipomoea*.

INTRODUCTION

Ipomoea, the largest genus in the Convolvulaceae is known globally for the sweet potato (*I. batatas*), the sixth most important starch crop of the world (faostat.fao.org). In addition to the sweet potato, the genus contains 600 to 1000 species (Austin & Huáman 1996; Manos et al. 2001), most of which occur in the New World with approximately 167 (25%) native to temperate and tropical North America (including Mexico). These species display a wide range of floral morphologies indicative of different pollinators and/or breeding systems (autogamy versus xenogamy; Fig. 1A–F, 2A–D). While recent molecular phylogenetic studies have included *Ipomoea* species (Miller et al. 1999; Manos et al. 2001, 2004; Miller et al. 2004), they have not used phylogenetic hypotheses to examine changes in breeding system. Similarly, numerous studies have described the breeding systems of various *Ipomoea* species (cf., Ennos 1981; Bullock et al. 1987; Devall & Thien 1992; Chang & Rausher 1998; Chemás & Bullock 2002) but have not set these studies into a comparative framework. Here we combine a phylogenetic study of North America *Ipomoea* with greenhouse studies of breeding systems of all taxa included to assess the occurrence of different breeding systems in an evolutionary context and examine the relationship between breeding systems and floral traits.

An historical and prevailing assumption that outcrossing (xenogamy) in flowering plants is responsible

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for the remarkable diversity and evolutionary success of the angiosperms (Darwin 1877; Stebbins 1974; Faegri & van de Pijl 1979) has been tempered in recent years by the recognition of high rates of autogamy in herbaceous groups (Barrett et al. 1996; Kohn et al. 1996; Schoen et al. 1997; Goodwillie1999; Richman & Kohn 2000; Lu 2001; Barrett 2002; Allem 2003; Igic et al. 2003) and the frequent occurrence of apomixis in tropical tree groups (Kaur et al. 1978; Allem 2003; Ashman & Majestic 2006). Since 20–30% of all flowering plant species produce offspring by means of self-fertilization (Barrett 2002; Allem 2003), there is ample evidence that self-compatibility confers a competitive edge over self-incompatibility under certain environmental conditions. Nevertheless, cross-fertilization is the favored mode of reproduction in most angiosperm groups, leading to a general consensus that cross-fertilization promotes heterozygosity and genetic polymorphisms in plant populations (Grant 1958; Faegri & van der Pijl 1979; Liu et al. 1998; Allem 2003), thereby facilitating adaptability to changing environments over the long course of evolutionary time (Holsinger 2000).

Evolutionary biologists recognize two different explanations for high rates of self-pollination among herbaceous angiosperm groups. The 'automatic selection' hypothesis states that alleles for self-compatibility within gene pools of outcrossing individuals will be inherited in larger proportions than self-incompatibility alleles (3:2) due to increased rates of transmission, this owing to the additive effects of both selfing and cross-fertilization mechanisms (Fisher 1941; Jain 1976; Schoen et al. 1996; Holsinger 2000). Alternatively, the 'reproductive assurance' hypothesis ascribes high rates of autogamy in plant populations of transitory and insular habitats (Baker 1955; Webb & Kelly 1993; Bernardello et al. 2001) to a filter mechanism that favors self-compatible disseminules and their ability to establish viable colonies in the absence of mates or pollinators after long-distance dispersal events (Baker 1955, 1967; Stebbins 1974; Lloyd 1980; Pannell & Barrett 1998).

Theoreticians agree that selfing advantages are counter-balanced by genetic benefits that derive from the process of cross-fertilization by increasing rates of pollen discounting and diminishing the expression of lethal homozygous deleterious alleles (Lande & Schemske 1985; Charlesworth & Charlesworth 1987; Harder & Wilson 1998). These predictions are substantiated by studies of natural plant populations, many of which conclude that perennial plant species are more susceptible to inbreeding depression than annuals on account of higher genetic loads (Lande & Schemske 1985; Charlesworth & Charlesworth 1987; Lloyd & Schoen 1992; Barrett et al. 1996; Liu et al. 1998; Holsinger 2000; Barrett 2002). While experimental crossing studies on both plants and animals support this perspective (Crnokrak & Barrett 2002), Lande and Schemske (1985) predict plant populations should be able to purge themselves of deleterious alleles by means of occasional selfing events within outcrossing populations. Populations must apparently pay, however, an initial competitive price in progeny success rates during the purgation process.

Shifts from outcrossing to inbreeding modes of reproduction are believed to be initiated by the malfunction of self-incompatibility mechanisms (Barrett 2002). If selfing behaviors prove advantageous, then selective forces will no longer favor floral characteristics that are associated with cross-pollination syndromes. Hence Barrett et al. (1996) recognize that outcrossing is usually associated with a number of floral features and syndromes that are attractive to pollinators, just as self-compatible flowers exhibit dysfunctional vestiges of these same features. They also note that co-variation of two or more floral characters between taxa can inform us about the adaptive significance of such features if we understand these attributes in the context of their phylogenetic and functional linkages.

In the present study we generate a phylogenetic hypothesis based on existing and newly-collected ITS sequence data for 70 North American *Ipomoea* taxa and use this phylogeny to pinpoint changes in breeding systems and associated changes in floral traits. Breeding systems for the species included were determined by experimental greenhouse studies. We also use these data to examine the impact of breeding system changes on floral structures. Most *Ipomoea* species present large and showy flowers and produce substantial amounts of nectar and pollen as attractants (Figs. 1, 2). In shifts from xenogamy to autogamy, one might expect the relaxation of selection pressures that maintain showy floral features and the increased influence

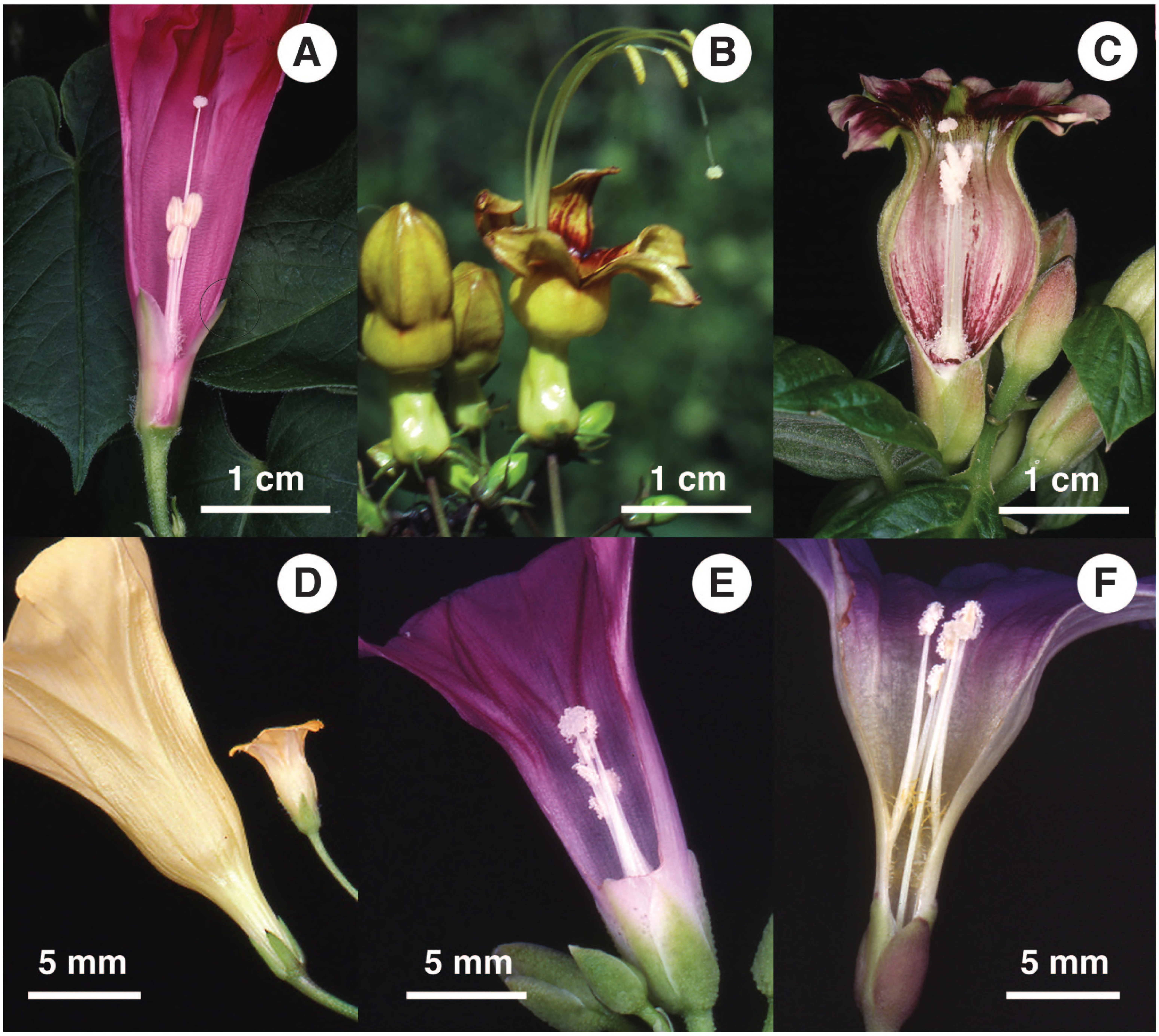

Fig. 1. Floral structures of assorted xenogamous (1–3) and autogamous (4–6) *Ipomoea* Species from North America. A. *Ipomoea orizabensis* var. *collina* is melitophilous, self-incompatible, and strongly herkogamous. B. The hummingbird pollinated species, *I. neei*, is both self-incompatible and strongly herkogamous. C. *Ipomoea gesneriodes* is somewhat unique in exhibiting herkogamous flowers, urceolate corollas, and subequal stamens. D. *Ipomoea microsepala* and *I. minutiflora*, the sole members of *Ipomoea* ser. *Microsepalae*, exhibit strong differences in flower sizes as xenogamous and autogamous species (respectively). E. *Ipomoea dumetorum* exhibits typical features of an autogamous species derived from a melitophilous ancestor. Note flowers are small (ca. 2.5 cm long) and stamens are subequal. The stigma maintains close contact with several anthers. F. *Ipomoea aristolochiaefolia* is an autogamous species that belongs to a group that is predominantly pollinated by hummingbirds or long-tongued flies (*I. Exogonium* s.l.). Note the flowers are small (ca. 2.5 cm long), the vestigial tube pronounced with adnate filaments, and the stamens subequal. The stigma maintains close contact with most anthers.

of mechanisms that enhance selfing abilities. We point out the relationships between breeding system and three floral traits: flower size (length), pollen:ovule ratio, and anther-stigma distance. The costly production of large flowers and large amounts of pollen is hypothesized to decrease in selfing lineages (Goodwillie et al. 2009) while the distance between anthers and stigma is hypothesized to decrease in order to facilitate selfing.

Although many studies have discussed relationships between breeding system and floral evolution (e.g., Cruden 1977, 2000; Lord & Eckhard 1984; Plitman & Levin 1990; Gallardo et al. 1994), this study represents the first attempts to understand these relationships within a phylogenetic context in *Ipomoea*. With an aim to examine the multiple origins of inbreeding in North American *Ipomoea*, we obtained DNA

Fig. 2. Contrastive floral features of closely related xenogamous and autogamous sister species of *Ipomoea* in North America. **A.** *Ipomoea variabilis* (*I.* sect. *Exogonium*) is xenogamous and shares a number of synapomorphic characteristics with the sister species, *I. meyeri* (late leaf primordia sub-bullate; sepals foliose and hispid, corolla tube basally yellow-pigmented). Like other outcrossing *Ipomoea*, this species has relatively large and colorful flowers, heteromophic stamens and style (herkogamous flowers), and high pollen-ovule ratios (Table 1). **B.** *Ipomoea meyeri* is autogamous and sister to *I. variabilis*. Flowers are relatively small (<2.5 cm long), stamens and style subequal, and pollen-ovule ratios low (Table 1). **C.** *Ipomoea tricolor* (*I.* sect. *Tricolores*) is xenogamous and shares a number of synapomorphic characteristics with the sister species, *I. cardiophylla* (sepals small, deltoid-elongate, papillate, corolla tube yellow). Like other outcrossing *Ipomoea*, this species has relatively large and colorful flowers, heteromophic stamens and style (herkogamous flowers), and relatively high pollen-ovule ratios (Table 1). **D.** *Ipomoea cardiophylla* is autogamous and exhibits flowers that are relatively small (<3 mm long), the stamens and style subequal, and low pollen-ovule ratios (Table 1).

sequences of about 90% of all known autogamous species in this region of the world and sampled xenogamous species that demonstrate phylogenetic affinities with inbreeding taxa on the basis of morphological characters. We measured several floral characteristics that have long been associated with inbreeding species in *Ipomoea*, including small corollas, subequal stamens and styles, and low pollen-ovule ratios, to examine the distribution of such these characteristics in a phylogenetic context and to discern multiple origins of these associative characteristics. The multiple and correlative origins of these characteristics are considered in an evolutionary context.

MATERIALS AND METHODS

Taxon Sampling

In order to obtain a broad sample of North American species and their close relatives, published ITS sequences of 50 species (47 *Ipomoea* and 3 outgroups) were acquired from GenBank (Manos et al. 2001; Miller et al. 2004) and an additional 23 xenogamous species of *Ipomoea* that demonstrate close relationships with inbreeding taxa on the basis of morphological synapomorphies, representing 21 species and 2 varieties, were sequenced. As a whole, these species comprise a substantial complement of taxa that fall within two subgenera of the genus (*I.* subg. *Eriospermum* and *Quamoclit*), representing 17 different sections and series (Table 1). The former subgenus comprises a paraphyletic assemblage of clades that include both New and Old World elements while the latter is monophyletic and consists predominantly of tropical North American taxa. Voucher specimens for a total of 73 Convolvulaceae are listed in Appendix 1 along with their collection localities and GenBank accession numbers.

We initially included samples from two or three populations of 25 species in our phylogenetic investigations, but duplicate accessions did not alter the topologies of trees from those including only a single population of each taxon. We therefore include only one sequence for each taxon in our final results.

Because various Mexican species of *Ipomoea* occupy a basal phylogenetic position within the Ipomoeae tribe (Miller et al. 1999, 2004), we employed three different outgroups of the sister tribe, Merremiaea (Stefanovic et al. 2002): *Merremia dissecta*, *Merremia tuberosa*, and *Operculina pteripes* (Appendix 1).

For newly sequenced species, DNA was extracted from fresh leaf material grown in greenhouse facilities at The University of Texas. Seeds were collected by the first author in the field or obtained from the USDA Southern Regional Plant Introduction Station, Griffin, Georgia.

DNA Extraction and Amplification

Whole genomic DNA was extracted by following a modified Doyle and Doyle (1987) protocol using a CTAB extraction buffer with 0.2% (v:v) beta-mercaptoethanol. The internal transcribed spacer (ITS) region of the 18S–26S nuclear ribosomal repeat was chosen for phylogeny reconstruction. We employed primers ITS 1A (5'GGA AGG AGA AGT CGT AAC AAG G 3') and ITS 4 (5'TCC TCC GCT TAT TGA TAT GC 3') as primers to amplify the ITS I, the 5.8s region, and ITS II via the polymerase chain reaction (PCR). Reaction volumes of 25 ul included 2.5µL of 10x Triton-X PCR buffer (final concentration 1x), 2µL 10mM dNTP mix (final concentration 0.8 mM dNTPs), 2 µL 25mM MgCl (final concentration 2mM MgCl), 1.25 µL DMSO (final concentration 5% v:v), 1 unit of Taq enzyme, and 0.25 µL 20µM forward and reverse primers (0.2µM final concentration of each primer). After initial denaturation at 95° C for 5 min, amplification proceeded at 94° C for 3 min, 46–52° C for 1 min, 72° C for 1 min, followed by 35 cycles of 94° C 1 min, 46–52° C 1 min, 72° C for 45 sec + 3 sec/cycle, with a final 7 min extension at 72° C. Amplification products were visualized on a 1.5% agarose gel stained with ethidium bromide and viewed with UV on a transilluminator. PCR products were cleaned prior to sequencing with QIAquick spin columns (Qiagen Inc.) according to the manufacturer's instructions.

Cycle sequencing was performed using Big Dye terminator chemistry and either the forward or reverse amplification primer. Centri-sep columns were used to remove residual salts and unincorporated nucleotides from the sequencing products. Automated sequencing was performed on a BaseStation sequencer (MJ GeneWorks, San Francisco, CA). Forward and reverse sequence strands were assembled and edited

Table 1. Tropical and Temperate North American Convolvulaceae observed under greenhouse conditions, including 86 species and two varieties of *Ipomoea* and three outgroup species of *Merremia* and *Operculina*. Detailed floral and reproductive characteristics of a sampling of *Ipomoea* and outgroups included in phylogenetic analyses (73 species and 2 varieties) are provided. Species followed by an **X** are recognized as xenogamous (< 20% viable seed set of non-treated flowers), those followed by an **A** as autogamous (>50% viable seed set of non-treated flowers), and those with **X/A** have a mixed mating system. Pollen/Ovule ratios (P/O) are recorded for selected species, most of which are based on the average measurement of 2–10 flowers. Floral characteristics of each species are scored as follows: **L** = large corollas, **S** = Small corollas; **He** = Herkogamous flowers (unequal stamens and style); **Ho** = Homomorphic (subequal) stamens and style. ITS sequence data reported by Miller et al. (1999; 2004) and Huang et al. (2002) are marked by a single asterisk (*) while new ITS sequence data are marked by two asterisks (**). Appendix 1 provides author names of binomials, voucher information, and GenBank numbers. The classification scheme follows a modified system of McDonald (1991) based on recent molecular studies by Miller et al. (1999; 2004).

	Breeding System	P/O	Corolla	Stamens
Subgenus Eriospermum				
Section *Eriospermum* H. Hallier				
Series *Anisomeres* (House) D.F. Austin				
I. squamosa	**X**		L	He
Series *Batatas* (Choisy) D.F. Austin				
I. batatas var. *batatas* *	**X**	922	L	He
I. batatas var. *apiculata***	**X**	744	L	He
*I. cordatotriloba**	**X/A**	476	L	He
*I. lacunosa***	**A**	159	S	Ho
*I. ramosissima***	**A**	198	S	Ho
*I. tabascana**	**X**	694	L	He
*I. tenuissima***	**A**	196	S	Ho
*I. tiliacea***	**X**	1069	L	He
*I. trifida***	**X**	741	L	He
*I. triloba**	**A**	151	S	Ho
*I. umbraticola**	**X**	1111	L	He
Series *Jalapae* (House) D.F. Austin				
*I. amnicola**	**A**	604	S	Ho
*I. fimbriosepala***	**A**	458	S	Ho
*I. jalapa***	**X**	1950	L	He
*I. leptophylla**	**X**	2175	L	He
*I. pandurata**	**X**		L	He
Series *Arborescentes* (Choisy) D.F. Austin				
*I. arborescens**	**X**		L	Ho
I. murucoides	**X**		L	Ho
*I. pauciflora***	**X**		L	Ho
I. populina	**X**		L	He
I. praecana	**X**		L	He
I. wolcottiana	**X**		L	Ho
Series *Setosae* (House) D.F. Austin				
*I. setosa***	**X**	1378	L	He
*I. sepacuitensis***			L	
Series *Microstictae* (unpubl.)				
*I. conzattii**	**X**		L	Ho
I. suaveolens	**X**		L	He
Series *Bombycospermae* (Presl) D.F. Austin				
I. bombycina	**X**		S	He
I. gesnerioides	**X**		L	Ho
Section *Erpipomoea* Choisy				
*I. pes-caprae**	**X**	2028	L	He
*I. imperati**	**X**	1873	L	He
Section or Series Unknown/Unpublished				
I. carnea Jacq. var. *fistulosa**	**X**	4584	L	He

Table 1. continued

	Breeding System	P/O	Corolla	Stamens
*I. clavata***	**A**	1172	L	Ho
I. corymbosa	**X**		L	He
*I. crinicalyx**	**X**		L	He
*I. hartwegii***	**X**		L	He
I. lenis	**X**		L	He
*I. pedicellaris**	**X**	1291	L	He
Subgenus *Quamoclit* (Moench) Clark				
Section *Pharbitis* (Choisy) Griseb.				
Series *Pharbitis* (House) D.F. Austin				
*I. ampullacea**	**X**	2413	L	He
*I. hederacea**	**A**	152	L	Ho
*I. indica**	**X/A**	887	L	He
I. laeta	**X**		L	He
*I. lindheimeri**	**X**	263	L	He
*I. mairetii**	**X**		L	He
*I. nil**	**A**	151	L	Ho
*I. neurocephala**	**A**		L	Ho
*I. pubescens**	**A**	155	S	Ho
*I. purpurea**	**X/A**	126	L	He
I. villifera	**X**		L	He
Series *Tyrianthinae* (House) D.F. Austin				
*I. ancisa***	**X**		L	
I. orizabensis var. *orizabensis**	**X**	905	L	He
I. orizabensis var. *collina***	**X**		L	He
*I. parasitica**	**A**	223	S	Ho
*I. stans**	**X**		L	He
*I. sesscossiana**	**X**		L	He
Section *Calonyction* (Choisy) Griseb.				
*I. alba**	**X**	1064	L	Ho
*I. santillanii**	**X**	3177	L	He
*I. muricata**	**A**	135	L	Ho
Section *Exogonium* (Choisy) Griseb.				
*I. aristolochiaefolia***	**A**	112	S	Ho
I. bracteata	**X**	405	L	Ho
*I. dumetorum**	**A**	90	S	Ho
I. dumosa	**X**	L		Ho
*I. expansa**	**X**	L		He
*I. meyeri***	**A**	118	S	Ho
I. puncticulata	**X**	L		He
*I. purga**	**X**	L		Ho
*I. seducta**	**X**	L		Ho
I. signata	**X**	L		He
*I. simulans***	**X**	591	L	He
I. suffulta	**X**		L	He
*I. variabilis***	**X**	1147	L	He
Section *Leptocallis* (G. Don) J.A. McDonald				
*I. chamelana**	**X/A**	108	S	He
*I. costellata***	**A**	63	S	Ho
I. tenuiloba var. *tenuiloba*	**X**	143	L	He
*I. ternifolia**	**X**	719	L	He

Table 1. continued

	Breeding System	P/O	Corolla	Stamens
Section *Mina* (Cerv.) Griseb.				
*I. cholulensis***	**A**	51	L	Ho
*I. coccinea**	**A**	80	L	Ho
*I. funis**	**X**		L	He
*I. hastigera**	**X**		L	Ho
*I. hederifolia**	**X/A**	134	L	Ho
*I. lobata**	**A**	383	S	Ho
*I. lutea**	**X**		L	Ho
*I. neei**	**X**		L	He
*I. quamoclit**	**A**	92	L	Ho
Section *Microsepalae* (House) D.F. Austin				
*I. microsepala***	**X**	735	L	He
*I. minutiflora***	**A**	51	S	Ho
Section *Tricolores* D.F. Austin				
*I. cardiophylla**	**A**	165	S	Ho
*I. tricolor**	**X**	726	L	He
Outgroups				
*Merremia tuberosa**	X	2674	L	He
*Merrmia dissecta**	X	5114	L	Ho
*Operculina pteripes**	X	11,871	L	He

in Sequencher 4.5. The sequences were aligned manually in MacClade (Maddison & Maddison 2000). Six variable sites were excluded due to ambiguous alignment (Treebase submission SN2687; Pin #6910). New sequences are available from GenBank (accession submission numbers DQ33303-355325, Appendix 1).

Phylogenetic Analyses

For phylogeny reconstruction, the ITS data set was analyzed in PAUP* 4.0b10 (Swofford 2002) using parsimony as the optimality criterion. Heuristic tree searches included 1,000 random addition replicates using MULPARS and tree-bisection-reconnection branch swapping (TBR). These trees were saved and used as the basis for another round of TBR swapping up to an arbitrary maximum of 20000 trees. A majority-rule and strict consensus tree were generated from these. Support for internal branches was determined by 1000 bootstrap replications (Felsenstein 1985) using the same heuristic search strategy.

The ITS data set was also analyzed using Bayesian methods implemented in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). The best-fitting model of sequence evolution was determined using ModelTest 3.7 (Posada & Crandall 1998) in PAUP 4.0b10 (Swofford 2002). Analyses in MrBayes 3.1.2 consisted of two Markov Chain Monte Carlo runs, each composed of four linked chains. The runs proceeded for 4 million generations, sampling every 100 generations. We identified the burn-in phase by examining the plot of log-likelihood scores for the two runs. Convergence was assessed by examining the standard deviation of split frequencies across chains and, more importantly, by similarities in topology, branch lengths, and clade credibilities between the two independent runs (Huelsenbeck et al. 2002).

Breeding System and Floral Morphology Data Collection

Reproductive behaviors of 89 taxa were observed directly in greenhouse facilities at The University of Texas (Table 1), accounting for more than half of North America species. Breeding systems were determined by observing spontaneous seed-set of untreated flowers (without emasculation or pollinators) within greenhouse settings. Species that consistently produced fewer than 20% seed set in the absence of pollinators were scored as xenogamous; those with over 50% seed set without pollinators were scored as autogamous.

Ten measurements of flower length and anther-stigma distance (herkogamy) were collected from either fresh or herbarium materials (TEX, UNAM). Pollen-ovule ratios for 51 of the 68 species were determined by counting the total number of pollen grains in five anthers of each flower and then dividing this sum by the total number of ovules (i.e., four in most *Ipomoea*, six for members of *I.* series *Pharbitis*; Table 1). When live material was available, an average pollen-ovule ratio was measured by directly observing and counting every pollen grain from a total of 10 flowers. Ratios obtained from herbarium specimens were based on measurements of 1–3 flowers. The herbarium sheet approximations of pollen-ovule ratios should prove reliable for the present survey, as formerly published measurements indicate pollen number within species varies from 1–10% (McDonald 1982; Chemás Jaramillo & Bullock 2002) while pollen-ovule ratios between sister autogamous and xenogamous species usually differ by factors that range from 100–2000% (Table 1).

We also collected data of all 68 species for three floral traits coded as discrete characters. Based on observation of living and herbarium materials at TEX, flowers with corolla tubes that exceed 2.5 cm in length were scored as 'large' while those that range from 0.5–2.5 cm in length were classified as 'small' (Table 1). Species were deemed herkogamous if anthers and stigma are separated spatially (usually by several millimeters).

We were not able to use methods currently available for predicting ancestral traits or for rigorous comparative analyses because we were able to sample only 41% of the species of North America and our sample is not truly random. However, we did code the floral and reproductive characters in Table 1 (autogamy versus xenogamy, herkogamy vs. homomorphic sexual structures, floral length, and pollen:ovule ratios) as discrete characters and then optimized them on the tree shown in Figure 3 using MacClade 4.08 (Maddison & Maddison 2005) under a parsimony criterion (Fig. 4A, B, Fig. 5 A, B).

RESULTS

Phylogeny estimation

The aligned matrix of ITS sequence data totaled 676 bp. Across these characters, 355 were variable and 221 were parsimony-informative. For the parsimony analysis, we excluded uninformative characters, leaving 221 characters analyzed. The parsimony analysis generated 120,950 equally most-parsimonious trees. The consensus of these trees was similar to that obtained from the Bayesian analysis.

For Bayesian analysis, the best-fitting model of sequence evolution for this dataset was a general time-reversible model with gamma-distributed rate variation and the number of invariant sites estimated. Both independent runs produced similar consensus topologies, suggesting convergence on the most probable area of tree space. The average standard deviation of split frequencies was less than 0.01 after the burn-in phase (30%), also indicating good convergence. The resulting majority-rule consensus of 56,000 trees is used (Fig. 3) for the assessment of the breeding system and floral morphology across the species.

Breeding System and Floral Trait Data

Greenhouse studies confirmed that *Ipomoea* species range from completely selfing (ca. 100% viable seed set in non-treated flowers) to completely outcrossing (0% viable seed set in non-treated flowers). Based on our scoring methods for an ingroup of 87 taxa (Table 1), 59 species were scored as xenogamous, 23 as autogamous, and 5 as having a mixed breeding system (self-compatible but facultatively herkogamous). Flowers of 69 taxa were scored as large and 18 as small. Distances between the anthers and stigma yielded 51 species being scored as herkogamous and 38 as homogamous.

Pollen:ovule ratios for the 51 species counted (Table 1) exhibited remarkable variability, ranging from 51–3177:1 (x = 597). High extremes of autogamous pollen-ovule ratios in *I. amnicola* (604:1) and *I. clavata* (1172:1) occasionally exceed the low extreme of pollen-ovule ratios in various xenogamous species (Table 1), such as those of *I. bracteata* (405:1) and *I. simulans* (591:1). In a similar fashion, several self-compatible, outcrossing species that produce herkogamous flowers, such as *I. chamelana* (P/O = 108), *I. cordatotriloba* (P/O = 476), and *I. hederifolia* (P/O = 134), exhibit pollen-ovule ratios that fall within limits of many autogamous species (Table 1).

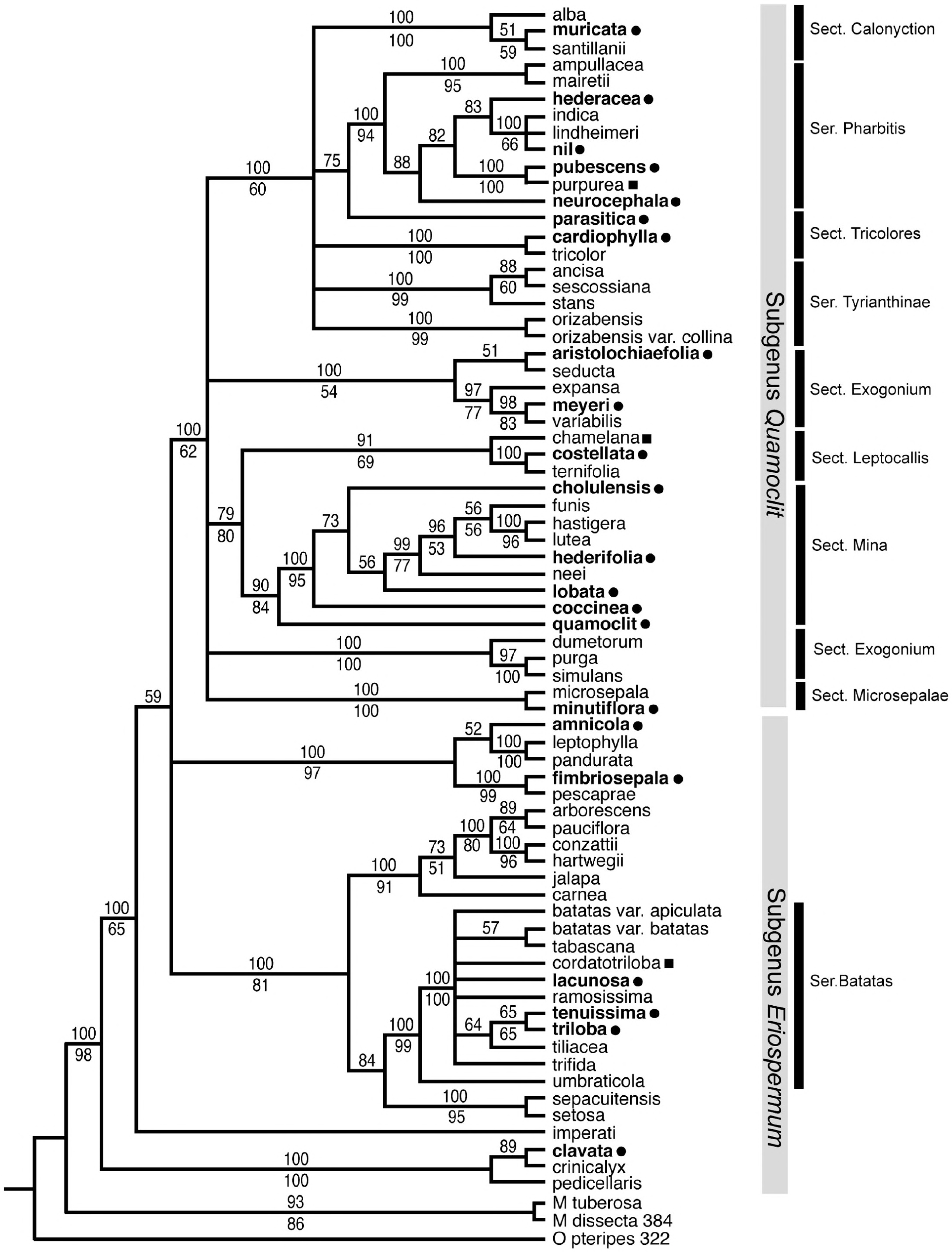

Fig. 3. Bayes consensus tree based on an analysis of ITS sequence data. Bold type and solid circles indicate autogamous lineages while xenogamous lineages are indicated by regular type and and no symbols. Names followed by a solid square box indicate self-compatible species that outcross facultatively on account of herkogamous flowers. Numbers above the branches are posterior probabilities from the Bayesian analysis. Numbers below the branches indicate bootstrap support for 1000 replicates. Sectional and series dispositions of species are indicated by bars to the right of the tree.

The results of the character optimization are shown in Figures 4 and 5. These optimizations reveal considerable congruency in character evolution. Herkogamy, long flowers and large pollen:ovule ratios usually occur on outcrossing lineages while homomorphic sexual structures, short flowers and small pollen:ovule ratios trace primarily along inbreeding clades.

DISCUSSION

The present study uses a new phylogenetic reconstruction for North American *Ipomoea* to explore breeding systems and their floral traits. Our analyses indicate multiple (potentially 16) independent transitions to autogamy and possibly reversals (Fig. 3). We found that apparent transitions between xenogamy and autogamy were strongly associated with changes in a suite of floral traits including flower size, distance between the anthers and stigma within a flower, and pollen:ovule ratio. Here we discuss the results in the context of existing studies of breeding system evolution and suggest avenues for future work.

Although a few phylogenetic studies based on morphological data suggest xenogamy may be a derived feature (Olmstead 1989; Armbruster 1993; Kelly 1997), almost all studies based on molecular evidence indicate that inbreeding lineages are derived from, and rarely revert back to, outcrossing habits (Barrett et al. 1996; Goodwillie 1999; Weller & Sakai 1999; Vieira & Charlesworth 2002; Igic et al. 2003). Similarly, our estimates based on a sample of 68 *Ipomoea* species suggest strong directionality in transitions, with many shifts from xenogamy to autogamy and a few in the reverse direction (notably *Ipomoea* sers. *Mina* and *Pharbitis*; Fig. 3).

Although most autogamous species appear as isolated tips in xenogamous clades, in a few cases autogamous species are closely related to other autogamous species, as observed among members of *Ipomoea* ser. *Pharbitis* (*I. pubescens* is sister to *I. purpurea*, *I. nil* is sister to *I. hederacea*), *Ipomoea* ser. *Batatas* (*I. lacunosa*, *I. cordatotriloba*, *I. ramosissima*), and particularly species in *Ipomoea* sect. *Mina*. Apart from these exceptional examples, however, autogamous lineages in *Ipomoea* appear to undergo cladogenesis less often than their most closely related xenogamous lineages, this being consistent with the notion that transitions to selfing may decrease speciation or increase extinction, leading to an evolutionary dead-end (Stebbins 1957; Takebayashi and Morrell 2001). Substantiating this pattern across *Ipomoea* will require, however, a broader sampling of taxa for statistical analyses, as discussed below.

The lack of species-rich clades in terms of autogamous taxa in *Ipomoea* compares closely with those of the Polemoniaceae but contrast significantly with inbreeding lineages of the Solanaceae. Self-compatible lineages have arisen at least 16 times in the Polemoniaceae and a large majority of these have failed to diversify over the course of time (Barrett et al. 1996). In contrast, an estimated 60% of species in the Solanaceae (ca. 1200 spp.) are identified as self-compatible, and these autogamous nightshades are often closely related to one another, comprising clades of exclusively inbreeding taxa (Igic et al. 2003). This distinction is noteworthy (and as yet unexplained in terms of their genetic architecture and evolutionary histories), as the Convolvulaceae are sister to Solanaceae and phylogenetically distant to the Polemoniaceae (Savolainen et al. 2000; Soltis et al. 2000).

Similar to evolutionary trends of autogamy in the Polemoniaceae (Barrett et al. 1996), selfing has arisen in distantly related groups of *Ipomoea* clades that exhibit a variety of pollination syndromes: i.e., hummingbird pollination (*I. cholulensis, I. hederifolia, I. neei, I. quamoclit*), bee pollination (*I. amnicola, I. cardiophylla, I. costellata, I. fimbriosepala, I. meyeri, I. leptophyla, I. microsepala, I. minutiflora, I. orizabensis, I. pubescens*, etc.), hawk-moth pollination (*I. neurocephala, I. muricata*), and long-tongued fly pollination (*I. aristolochiaefolia*, Fig. 1; McDonald 1982, 1991). Consequently, there is little evidence that specific animal vectors predispose or preclude a plant population's ability to become autogamous.

Inbreeding species in *Ipomoea* commonly possess a suite of floral characteristics that apparently arise convergently. These characteristics include relatively small (tubes usually < 2.5 cm long) and pale corollas, subequal stamens, anthers that make direct contact with the stigma (Fig. 1 E & F, Fig. 2 B & D), and low pollen:ovule ratios. Similar floral syndromes typify autogamous elements in various genera of the

Polemoniaceae (Grant 1981; Barrett et al. 1996), *Dalechampia* (Armbruster 1993), *Scutellaria, Mazus* and *Hosta* (Ushimaru & Nataka 2002), and often concomitant with a reduction in flower size in *Amsinckia*, *Limnanthes,* and *Epilobium* (Ornduff & Crovello 1968; Olmstead 1989; Parker et al. 1995; Schoen et al. 1997).

Our results suggest that shifts between autogamy and xenogamy are strongly correlated with simultaneous changes in flower size, pollen-ovule ratio, and anther-stigma distance (Table 1, Fig. 4A, B, 5A, B). Small autogamous flowers with anthers that touch stigmas and relatively low pollen-ovule ratios have arisen independently in numerous unrelated clades, including those comprising *Ipomoea* ser. *Batatas* (*I. triloba*), *I.* sect. *Calonyction* (*I. muricata*), *I.* sect. *Exogonium* s. lat. (*I. aristolochiaefolia*, *I. dumetorum*, and *I. meyeri;* Fig. 1 F&E, Fig. 2 B), *I.* sect. *Microsepalae* (*I. minutiflora*; Fig. 1 D), *I.* sect. *Mina* (*I. hederifolia*), *I.* ser. *Pharbitis* (*I. neurocephala*), *I.* sect. *Tricolores* (*I. cardiophylla*; Fig. 2 D), and *I.* sect. *Jalapae* (*I. amnicola*; see Table 1, McDonald 1982, 1991; Chemás Jaramillo & Bullock 2002). Such characteristics contrast with typical floral features of xenogamous relatives, whose flowers are normally large, brightly pigmented, herkogamous (Fig. 1 A–C, Fig. 2 A, C), and exhibit high pollen-ovule ratios (Table 1).

Pollen:ovule ratios can serve as a reliable indicator of breeding system. High pollen-ovule ratios are normally associated with obligate outcrossing behaviors, moderate pollen-ovule ratios with facultatively xenogamy, and low ratios with obligate autogamy (Cruden 1977, 2000; Lord & Eckhard 1984; Plitman & Levin 1990). As noted earlier, pollen-ovule ratios in our broad sampling of both autogamous and xenogamous taxa within *Ipomoea* varied considerably from 51–3100 grains per ovule (McDonald 1982; Chemás Jaramillo & Bullock 2002, Erbar & Langlotz 2005), and therefore provide a model system to examine this variation in a phylogenetic context. Most xenogamous taxa produced more than 400 pollen grains per ovule, roughly 2–14 times their autogamous relatives (Table 1). Lower pollen-ovule ratios (51–223:1) were invariably associated with autogamous relatives and lineages (Table 1; Fig. 3). While some autogamous species, such as *I. amnicola*, *I. clavata*, and *I. fimbriosepala* in *Ipomoea* subg. *Eriospermum*, exhibited relatively high pollen-ovule ratios (458–1172:1), these values are still 4–5 times lower than their closest xenogamous relatives [i.e., *I. leptophylla* (2175:1) and *I. setifera* (2971:1)]. Hence the quantitative relationship between pollen-ovule ratios of outcrossing and inbreeding taxa is not measurably precise, but predictably disparate in relative terms between closely related autogamous and xenogamous species.

While this study has focused on the evolution of floral traits associated with autogamy, other traits, such as life histories, are likely to be associated with shifts in breeding system. For example, a considerable portion of selfing *Ipomoea* species are annuals and share close ancestry with a xenogamous and (usually) perennial species (Fig. 3). Such associations are exemplified by the following species-pairs: *I. costellata* and *I. ternifolia*; *I. muricata* and *I. santillanii*; *I. purpurea* and *I. pubescens*; I. *cardiophylla* and *I. tricolor* (Fig. 2 C & D); *I. minutiflora* and *I. microsepala* (Fig. 1D); *I. meyeri* and *I. variabilis* (Fig. 2 A & B); *I. dumetorum* and *I. simulans*/*I. purga*; *I. fimbriosepala* and *I. pes-caprae*, and *I. amnicola* and *I. pandurata*/*I. leptophylla*.. Exceptions to this pattern include several selfing perennials, such as *I. amnicola*, *I. clavata*, and *I. fimbriosepala*, which belong to the woody and hairy seeded *Ipomoea* subgenus *Eriospermum* (*sensu lato*, Fig. 3; Table 1).

Additional research might consider the genetic and evolutionary mechanisms by which these autogamous lineages have arisen from xenogamous ancestors. Self-compatibility probably arises independently by unique point mutations at the S-locus (Kowyama et al. 2000), and the convergent evolution of floral syndromes associated with inbreeding habits likely arises secondarily and independently on account of shifts in selective forces on flower phenotypes. Without positive selection for floral features that attract and reward animal vectors, selection will favor floral reductions that allow more resource allocation for growth and seed production (Cruden & Miller-Ward 1981; Charnov 1982; Williams & Rouse 1990; Kirk 1992; Barrett et al. 1996; Goodwillie 2009). Therefore, autogamous species tend to produce relative smaller flowers that are less vivid in color (Richards 1997; Tate & Simpson 2004). The repeated evolution of the same suite of floral characters in association with selfing presents the opportunity to examine how often parallel trait evolution is caused by parallel genetic mechanisms.

Finally, *Ipomoea* offers a prime system for testing the effects of breeding system transitions on the fate

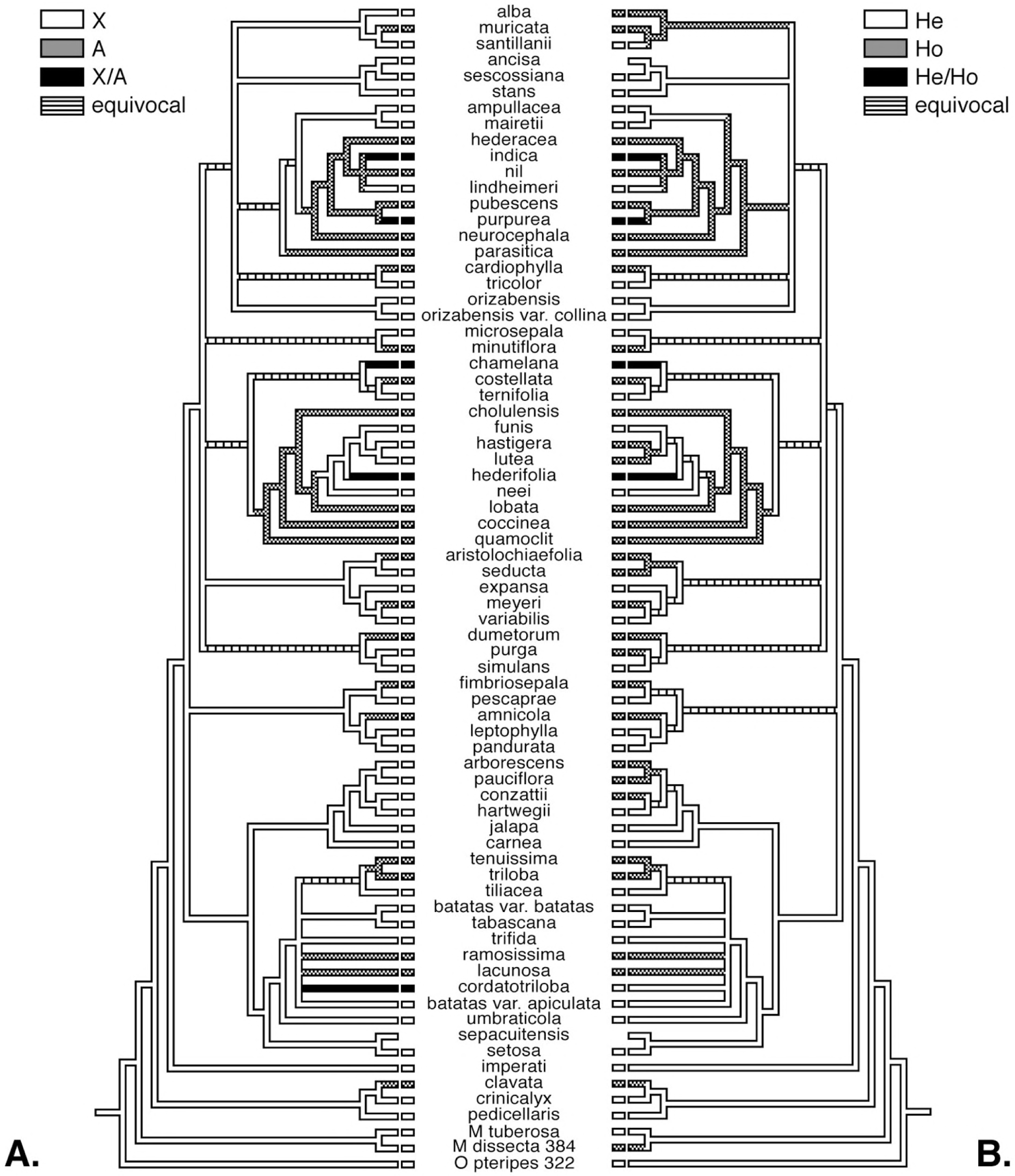

Fig. 4. Optimizations of breeding system and floral characters on the tree shown in Fig. 3. A. Breeding systems: xenogamy (X), autogamy (A), or mixed (XA). B. Anther and stigma separation: herkogamy (He), Homogamy (Ho), or mixed (He, Ho).

of lineages. Recently developed models by Maddison et al. (2007) make it possible to test statistically the effect of a binary character on rates of speciation and extinction. With such methods, one can determine whether selfing lineages diversify less than outcrossing lineages and whether the differences in species richness between the selfers and outcrossers is attributable to differential extinction, speciation, or both of these processes. Although these analyses will require more intensive taxon sampling, they hold the possibility of determining whether transitions to selfing represent evolutionary dead-ends.

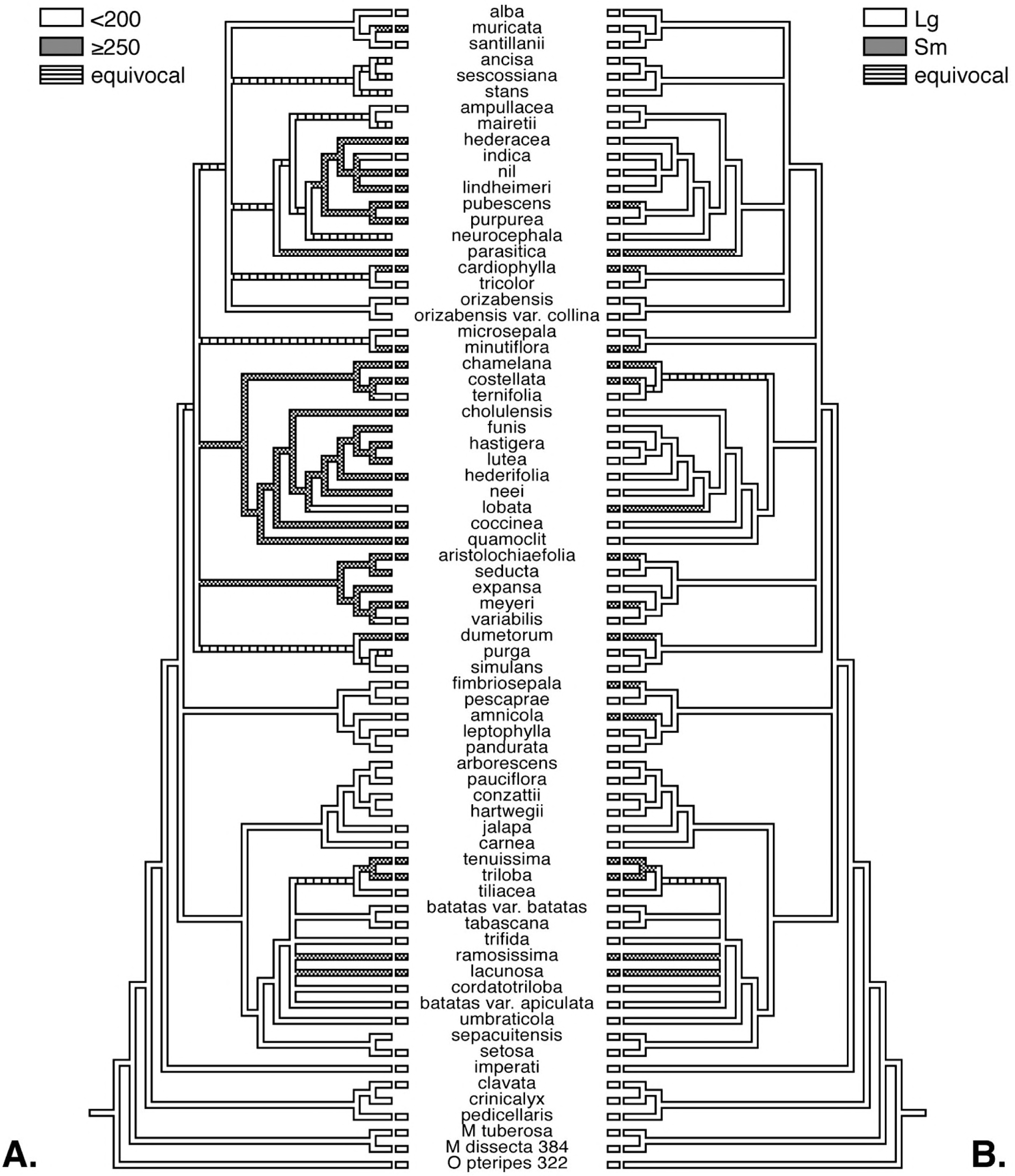

Fig. 5. Optimizations of breeding system and floral characters on the tree shown in Fig. 3. A. Pollen:ovule ratio with ratios below 250 (Table 1) as one discrete class, values above 250 as the second class, and a third class as equivocal values. B. Corolla size scored as large, small, or equivocal.

The correspondence of outcrossing features on outcrossing clades as shown in figures 4 and 5 appears to be strongest with respect herkogamy vs. homomorphic styles and stamens, while a relatively weaker correspondence is observed in pollen:ovule ratios and corolla lengths. Exceptions to the evolution of correlative characters in the latter characteristic can be attributed to various factors. As regards corolla length, for example, a less consistent correspondence between relatively large corollas and inbreeding behaviors in *I. muricata* (*Ipomoea* sect. *Calonyction*; Figs. 3, 5) and various species in *Ipomoea* sect. *Mina* (i.e., *I. quamoclit, I.*

coccinea, *I. cholulensis*; Figs. 3, 5) can be attributed to the unique pollination syndromes of these two groups (hawkmoth and hummingbird pollination syndromes, respectively), whose outcrossing relatives generally present extraordinarily long and narrow corolla tubes. Alternatively, relatively less congruency is observed in pollen:ovule ratios (Fig. 5) and breeding systems on account of our incomplete data set for pollen counts and an exceedingly wide range of variation in this floral parameter. Nevertheless, character optimization analyses generally reveal consistent phylogenetic correlations between autogamy, homomorphic sexual structures and low pollen:ovule ratios.

APPENDIX 1

Voucher and DNA sample information on *Ipomoea* species examined for ITS sequence variation, including (in order): taxon examined, DNA accession number, plant locality, collector, and GenBank accession number. McDonald vouchers are located at XAL or TEX; Miller vouchers are maintained at Southeastern Louisiana University (SLU), Hammond, Louisiana. Germplasm from SRPIS (USDA-Southern Regional Plant Introduction Station, Griffin, Georgia) provided fresh material. GenBank accession numbers for new sequences are presented in **boldface.**

Outgroup. *Merremia tuberosa* (L.) Rendle, REM 19, Unknown, Miller 8 (SLE), AF110909; *Merrmia dissecta* (Jacq.) Hallier *f.*, REM 384, Chihuahua, Mexico, *Miller 305*, GQ388262; *Operculina pteripes* (G. Don) Odonell, REM 322, Jalisco, Mexico, *Miller 365*, GQ388263.

Ingroup. *I. alba* L., REM 129, Oaxaca, Mexico, *McDonald 1926* (SLE), AF538275; *I. amnicola* Morong., REM 3, SRPIS-538265, Texas, USA, *Miller 3* (SLE), AF110928; *I. ampullacea* Fernald, REM 124, Jalisco, Mexico, *Lott 2362* (MEXU), AF538277; *I. ancisa* H. H. House, REM 11, Sonora, Mexico, *van Devender 97-1263* (TEX), **DQ355304;** *I. arborescens* (H.B.K.) G. Don, REM 38, SBE Universal Seedbank, *Miller 84* (SLE), AF110924; *I. aristolochiifolia* G. Don, JAM 6, Jalisco, Mexico, *McDonald 238* (TEX), **DQ355309;** *I. batatas* (L.) Lam. var. *batatas,* REM 1, SRPIS- 561558, Mexico, *Miller 39* (SLE), AF110938; *I. batatas* (L.) Lam. var. *apiculata* (M. Martens & Galeotti) J.A. McDonald & D.F. Austin, JAM 33, Veracruz, Mexico, *McDonald 1949* (TEX), **DQ355319;** *I. cardiophylla* A. Gray, REM 134, New Mexico, USA, *McDonald 141* (SLE), AY538280; *I. carnea* Jacq. var. *fistulosa* (M. Mart. ex Choisy) D.F. Austin, B&T World Seeds – 1472, *Miller 6* (SLE), AF 110920; *I. chamelana* J.A. McDonald, REM 153, Jalisco, Mexico, *McDonald 1930* (SLE), AY538281; *I. cholulensis* H.B. & K, JAM 2, Veracruz, Mexico, *McDonald 1886* (TEX), **DQ355305**; *I. clavata* v. Ooststr. ex Macbride, JAM 30, Veracruz, Mexico, Lascurrain s.n. (TEX), **DQ355325**; *I. coccinea* L., REM 13, North Carolina, USA, *Miller 47* (SLE), AF110941; *I. conzattii* Greenm., REM 44, B&T World Seeds-32404, *Miller 71* (SLE), AF110927; *I. cordatotriloba* Dennstedt, REM 52, B&T World Seeds-74931, *Miller 73* (SLE), AF110939*; I. costellata* Torr., JAM 1, Sonora, Mexico, *van Devender 20001-859* (TEX), **DQ335306**; *I. crinicalyx* S. Moore, WMC 8329, Jalisco, Mexico, *Bullock 2000* (Kew), AF309164; *I. dumetorum* Willd. ex Roem. & Schult., REM 147, New Mexico, USA, *McDonald 140* (SLE), AF538284; *I. expansa* J.A. McDonald, REM 135, Guerrero, Mexico, *McDonald 1910* (SLE), AY538285; *I. fimbriosepala* Choisy, JAM 44, Veracruz, Mexico, *Calzada 5985* (XAL), **DQ355315;** *I. funis* Schlecht. & Cham., REM 123, Guerrero, Mexico, *McDonald 1895* (SLE), AY538286; *I. hastigera* H.B.K., REM 139, Veracruz, Mexico, *McDonald 1998* (SLE), AY538287; *I. hartwegii* Benth., JAM 13, Querétaro, Mexico, *Carranza & Silva 6355* (TEX), **DQ335313**; *I. hederacea* Jacq., REM 163, Georgia, USA, *Miller 330* (SLE), AY538291; *I. hederifolia* L., REM 183, Mexico, Miller 318 (SLE), AY538294; *I. imperati* (Vahl) Griseb., North Carolina, USA, *Miller 99* (SLE), AF110917; *I. indica* (Burm. f.) Merr., REM 168, Madagascar, *Miller 256* (SLE), AY538297; *I. jalapa* (L.) Pursh, JAM 29, Tamaulipas, Mexico, *McDonald 1288* (XAL), **DQ335316**; *I. lacunosa* L., JAM 20, Missouri, USA, *Brant 4182* (TEX), **DQ335324**; *I. lindheimeri* A. Gray, REM 25, SPRIS-553011 (Texas, USA), *Miller 31* (SLE), AF110944; *I. leptophylla* Torr., REM 4, SRPIS-303327, *Miller 30* (SLE), AF110929; *I. lobata* (Cerv.) Thellung, REM 39, B & T World Seeds – 34004, *Miller 7* (SLE), AF110940; *I. lutea* Hemsl., REM 141, Chiapas, Mexico, *McDonald 1994* (SLE), AF538299; *I. mairetii* Choisy, REM 137, Chiapas, Mexico, *McDonald 2024* (SLE), AY538300; *I. meyeri* (Spreng.) G. Don, JAM 3, Jalisco, Mexico, *McDonald 1939* (TEX), **DQ335311;** *I. microsepala* Benth., JAM 4, Oaxaca, Mexico, *Elorsa 2801* (TEX), **DQ335307;** *I. minutiflora* (M. Mart. & Galeotti) House, JAM 5, Mexico, Mexico, *McDonald 174* (TEX), **DQ335308**; *I. muricata* Cav. REM 144, Jalisco, Mexico, *McDonald 1940* (SLE), AY538332; *I. neei* (Spr.) O'Donell, REM 140, Jalisco, Mexico, *Bullock & Martijena 2098* (SLE), AF538302; *I. neurocephala* Hallier, REM 145, Michoacan, Mexico, *McDonald 1963* (SLE), AY538303; *I. nil* (L.) Roth, REM 195, New Mexico, USA, *Miller 264* (SLE), AY538308; *I. orizabensis* (Pell.) Led. ex Steudl. var. *orizabensis,* REM 142 (SLE), Veracruz, Mexico, *McDonald 2434*, AY538309; *I. orizabensis* (Pell.) Led. ex Steudl. var. *collina* (H. H. House) J.A. McDonald, JAM 12, Nuevo Leon, Mexico, *Hinton 23668* (TEX), **DQ335303;** *I. pandurata* (L.) G. Mey., REM 48, Durham Co., North Carolina, *Miller 98* (SLE), AF110930; *I. parasitica* (H.B.K.) G. Don, REM 179, Morelos, Mexico, *Miller 333* (SLE), AY538313; *I. pauciflora* M. Mart. & Galeotti, JAM 25, Puebla, Mexico, *McDonald 2010* (XAL), **DQ335314**; *I. pedicellaris* Benth*.,* REM 97, Mexico, *Miller 185* (SLE), AF309165; *I. pes-caprae* L., REM 8, Kew Botanical Garden (Mali), *Miller 51* (SLE), AF110932; *I. pubescens* Lam., REM 76, Mexico, *Miller 113* (SLE), AF538314; *I. purga* (Wender.) Hayne, REM 133, Veracruz, Mexico, *Linajes s.n*. (SLE), AY538315; *I. purpurea* (L.) Roth, REM 171, North Carolina, USA, *Miller 254* (SLE), AY538322; *I. quamoclit* L., REM 167, Surinam, *Miller 181* (SLE), AF538323; *I. ramosissima* Choisy, JAM 56, Guanacaste, Costa Rica, *Moraga 604* (MO), **DQ335323;** *I. santillanii* O'Donell, REM 138, Veracruz, Mexico, *McDonald 1946* (SLE), AY538324; *I. seducta* House, REM 146, Chiapas, Mexico, *McDonald 1986* (SLE), AY538325; *I. sepacuitensis* Donn. Sm., JAM 61, Chiapas, Mexico, *E. Martinez S. 16636* (TEX), **DQ335317;** *I. sescossiana* Baillon, REM 143, Zacatecas, *McDonald s.n*., AY538326; *I. setosa* Ker Gawl., JAM 47, SRPIS 6162, *Griffin 6162*, **DQ335318;** *I. simulans*

Hanbury, JAM 9, Nuevo Leon, Mexico, *Patterson 6095* (TEX), **DQ335312;** *I. stans* Cav., REM 136, Puebla, Mexico, *McDonald s.n.* (SLE), AY538327; *I. tabascana* J.A. McDonald & D.F. Austin, Tabasco, Mexico, SRPIS (518479), AF256622, AF256623; *I. tenuissima* Choisy, JAM 49, Florida, USA, SRPIS (553012), **DQ355322;** *I. ternifolia* Cav., REM 47, B & T World Seeds – 64552, *Miller 78* (SLE), AF110942; *I. tiliacea* (Willd.) Choisy, JAM 34, Quintana Roo, Mexico, *McDonald 2020* (TEX), **DQ335321;** *I. tricolor* Cav., REM 16, Shepherd's Garden Seed, *Miller 52* (SLE), AF110936; *I. trifida* (H.B.K.) G. Don, JAM 38, Oaxaca, Mexico, *McDonald 2222* (TEX), **DQ335320;** *I. triloba* L., DLP2943, Mexico, Huang 14, AF256636, AF256637; *I. umbraticola* H.H. House, REM 29, SRPIS-561557, *Miller 24* (SLE), AF110836; *I. variabilis* (Cham. & Schlecht.) Choisy, JAM 10, Chiapas, Mexico, *McDonald s.n.* (TEX), **DQ335310.**

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BOOK REVIEW

Ray Neyland. 2009. **A Field Guide: Wildflowers of the Coastal Plain.** (ISBN 978-0-8071-3407-8, hbk). Louisiana State University Press, 3990 West Lakeshore Drive, Baton Rouge, Louisiana 70808, U.S.A. (**Orders:** Longleaf Services, Inc., 116 S. Boundary Street, Chapel Hill, North Carolina 27514-3808, U.S.A.; http://www.lsu.edu/lsupress/bookPages/9780807134078.html; customerservice@longleafservices.org; 800-848-6224; 800-272-6817 fax). $34.95, 339 pp., 535 color plates, 65 line drawings, 1 map, 9¼" × 6¼".

Neyland provides information on 535 species of herbaceous plants for the extensive coastal plain. The area encompasses the Gulf Coast eastward from Texas to southern Florida (excluding the southernmost tip), including the Mississippi River Valley flood plain from Illinois to the Gulf, and the Atlantic coast from Florida to New Jersey, Long Island, and Cape Cod.

The close-up photos of the flowers are beautiful and show excellent detail. However, it is difficult to estimate the size of the flower or the plant from a photo, and Neyland rarely describes the size of either.

Most pictures do not show leaf detail or sometimes no leaf at all is shown. This is frustrating, especially to the beginner, because the description of the leaves lacks important details, such as size, and contains terminology that may be unfamiliar.

Neyland often gives information about the root system, and whether it is annual or perennial, but does not include pertinent information about the plant above ground which is what most people would be looking for, such as size of the leaf, flower, and overall size of the plant. He also does not mention color variations although sometimes does allude to similar species.

He is vague about the bloom period, just giving a season, such as spring.

All of the information is in one paragraph without indentations so picking out some detail is time consuming.

The title of this book is Field Guide. In my opinion, this is a vague field guide. Neyland seems to provide a lot of information, but the details are mixed between a field guide format and a more advanced book on botany. He gives the scientific name and who named it. The origin of the name is interesting, and pertinent to a botanist or taxonomist, but does not need to be in a field guide. The space devoted to that information could be better used in a more detailed description of the plant itself.

The dichotomous keys are wonderful! They start logically with the color of the flower. However, I think they should be in the front of the book. This should be the starting point to identify an unknown flower.

The line drawings with identification of plant parts and terminology are great and provide valuable information for the beginning botanist. The glossary is very helpful also.

The flowers are arranged alphabetically by family name. For the experienced enthusiast this is acceptable, but might be intimidating for the beginner since the dichotomous keys are in the back. If you picked up the book and flipped through it, you might not buy it because at first glance it looks a bit technical.

Having pointed out the weaknesses of the book as a field guide, I would like to say that I would buy it for myself. The book is a convenient size to carry into the field and seems rather waterproof. I would therefore recommend it to an experienced wildflower observer or a botanist, but would not recommend it to a beginner unless that person is earnest and committed to really studying and learning family names of plants, scientific names, and plant terminology.—*Martha Mullens (educator, retired, and Master Naturalist), volunteer, Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A.*

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PUTATIVE MORPHOLOGICAL SYNAPOMORPHIES OF SAXIFRAGALES AND THEIR MAJOR SUBCLADES

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ABSTRACT

Putative morphological synapomorphies of Saxifragales, as currently circumscribed on the basis of molecular data, and of the major clades within this order, are hypothesized on the basis of a survey of morphological characters assessed from herbarium specimens. These characters were mapped with MacClade onto a well-resolved cladogram constructed using extensive DNA sequence data. Saxifragales possess unusual basifixed anthers, often with the filament attached at a basal pit. All but *Peridiscus* are united by their latrorse anther dehiscence and follicle fruits, the latter a feature that correlates with the ovaries being at least distally distinct. The woody clade (Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, and Hamamelidaceae) is diagnosed by adaxially flattened petioles, polytelic inflorescences, sessile flowers, and the loss of floral nectaries. Core Saxifragales (all members of the clade except Peridiscaceae, Paeoniaceae, and the woody clade) are united by the presence of a hypanthium (except for Crassulaceae). Phylogenetically useful morphological characters, although homoplasious, diagnose most major clades within the order, and these characters represent nearly all plant parts (e.g., vegetative morphology, floral and fruit morphology, and pollen structure). This analysis shows the utility of morphological analysis to reveal synapomorphies for major clades of angiosperms.

Key Words: Saxifragales, morphological phylogenetics, pollen structure

RESUMEN

Se plantean hipótesis de las sinapomorfías putativas morfológicas de Saxifragales, como se circunscriben en base a datos moleculares, y de los clados mayores dentro de este orden, en base a un estudio de caracteres morfológicos a partir de especímenes de herbario. Estos caracteres se procesaron con MacClade dando como resultado un cladograma bien resuelto construido mediante datos de secuencias extensas de DNA. Las Saxifragales posseen las poco frecuentes anteras basifijas, a menudo con el filamento unido a la fosa basal. Todos excepto *Peridiscus* están unidos por la dehiscencia latrorsa de la antera y frutos en folículo, esta última una característica que se correlaciona con los ovarios distintos al menos apicalmente. El clado leñoso (Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, y Hamamelidaceae) se diagnostica por sus peciolos aplanados adaxialmente, inflorescencias politélicas, flores sésiles, y la pérdida de nectarios florales. El núcleo de Saxifragales (todos los miembros del clado excepto Peridiscaceae, Paeoniaceae, y el clado leñoso) están unidos por la presencia de un hipanto (excepto Crassulaceae). Los caracteres morfológicos útiles filogenéticamente, aunque son homoplásicos, diagnostican los clados mayores dentro del orden, y estos caracteres representan casi todas las partes de la planta (ej., morfología vegetativa, floral y del fruto, así como la estructura del polen). Este analysis muestra la utilidad de los análisis morfológicos para poner de manifiesto sinapomorfías en los clados mayores de angiospermas.

As part of the Angiosperm AToL project, which resulted in a phylogenetic analysis of 640 species representing 330 families based on 25,260 aligned base pairs from 17 genes, representing all three plant genomes (Soltis et al., 2011), one goal was to assess morphological synapomorphies for each of the major clades of angiosperms. We present here a morphological exploration of Saxifragales, which represents the first treatment in a series of analyses (Judd et al., unpublished data) that will address morphological synapomorphies and the clades they support. Our data almost exclusively come from original observations taken directly from herbarium specimens representing the same species used in the molecular analyses and allow us to assess the morphological diagnosability of an array of large angiosperm clades, such as Saxifragales, based on easily

acquired morphological characters. This study, therefore, provides an example and a test for methods that we will soon apply across our large sampling of angiosperms.

This is the first analysis to explicitly assess morphological traits and potential synapomorphies across Saxifragales, which only recently has been recognized in its current circumscription, and represents an ancient and rapid diversification within the angiosperms (Angiosperm Phylogeny Group 2009; Fishbein et al. 2001; Jian et al. 2008; Kubitzki 2007a; Soltis et al. 2000, 2005, 2007). We note, however, that the phylogenetic analyses of Hermsen et al. (2006) employed both morphological and molecular characters, but these were not explicitly mapped onto the tree, since the focus of their paper was on the placement of fossil taxa.

MATERIALS & METHODS

Morphological characters and character states (Tables 1, 2) were determined from herbarium material at FLAS and MO, supplemented by reports from the literature. Most observations were made using a Wild stereomicroscope and attached Nikon 8700 digital camera. Observations of pollen and androecium characters were also made using an Hitachi S-4000 scanning electron microscope (SEM) at a running voltage of 5–7 kV. Pollen and stamens used for SEM were taken directly from herbarium sheets, mounted on aluminum stubs with adhesive graphite tabs, and coated with a gold-palladium alloy for 60 s. Metadata were input into TOLKIN (Beaman & Cellinese 2010).

Sixty-three morphological features (Table 1) were used to construct a character matrix (Table 2) in MacClade v.4.08 for Mac OS X (Maddison & Maddison 2000). Characters then were mapped using parsimony (Brokaw & Hufford 2010; Soltis et al. 2005) onto the cladogram of Saxifragales published by Jian et al. (2008; see their Fig. 1) using particular species of representative genera as terminals (Fig. 1; Table 3). This topology differs in a few minor ways from that recovered in the 17-gene analysis of angiosperms (Soltis et al., 2011). We used only *Liquidambar* L. to represent Altingiaceae because *Liquidambar* and *Altingia* Noronha are not reciprocally monophyletic, and only *Peridiscus* Benth. represented Peridiscaceae. In addition, we took into account the morphological character states seen in *Crassula* (Crassulaceae) and *Pterostemon* Schauer (Pterostemonaceae; sister to Iteaceae) using the phylogenetic placements of those two supported in the analyses of Jian et al. (2008). Vitaceae (represented by *Leea* Royen ex L. and *Vitis* L.) were used as an outgroup, and we note that the polarity of a few characters is equivocal.

Observations of wood anatomy were taken from the Inside Wood online database (http://insidewood.lib.ncsu.edu/). Vitaceae wood was so autapomorphic, due to its liana habit, that *Peridiscus* was used as a functional outgroup for the anatomy of the rest of the Saxifragales.

RESULTS

Potential synapomorphies for Saxifragales include basifixed anthers, with the filament attached at a basal pit in several groups (Fig. 2A–C; char. #42-1), but reversals to the dorsifixed condition (Fig. 2D-E) have occurred, and under DELTRAN optimization would be placed on the lineage leading to *Ribes* L., and at the common ancestor of the *Pterostemon* + Iteaceae clade (see also Fig. 1). Additionally, the presence of violoid to theoid teeth (char. #18-1) is possibly synapomorphic for Saxifragales, but salicoid teeth occur in *Aphanopetalum* Endl., and non-glandular teeth occur in *Hamamelis* L., *Itea* L., and *Haloragis* Forst. & Forst. f., while the condition cannot be assessed in taxa with entire leaves. All but Peridiscaceae are united by follicular fruits (char. #60-2) but this feature shows extensive homoplasy and is correlated with ovaries being at least distally distinct. All but Peridiscaceae also are united by latrorse anther dehiscence (Fig. 2B; char. #44-2, when ACCTRAN optimization is assumed), but this character also is quite homoplasious.

The woody clade (i.e., Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, and Hamamelidaceae; see Soltis et al. 2005) can be diagnosed by the flattened adaxial surface of the petiole (Fig. 3A; char. #14-1, but a grooved petiole occurs in *Cercidiphyllum* Sieb. & Zucc., and adaxially flattened petioles have evolved in parallel in *Choristylis* Harv. and *Kalanchoe* Adans.), polytelic or racemose inflorescences (char. #21-1, also evolving in parallel in *Peridiscus*, *Ribes* L., *Itea*, *Myriophyllum* L., and *Tetracarpaea* Hook.), and the loss

TABLE 1. Morphological characters and character states mapped onto molecular-based phylogeny of Saxifragales (see Jian et al. 2008). Putative plesiomorphic states listed first (coded as 0), followed by unordered apomorphic states (coded as 1, 2, 3, etc.).

No.	Morphological character and states
1.	Secondary growth: woody (0); herbaceous (1)
2.	Stem architecture: erect, not regularly rooting at nodes (0); prostrate, rooting at nodes (1)
3.	Stem dimorphism: absent (monomorphic), all stems erect (0); present, short and long shoots (1); present, erect aerial stems and horizontal underground rhizomes (2)
4.	Resinous compounds: absent (0); present (1)
5.	Leaf structure: monomorphic (0); dimorphic (1)
6.	Leaf position and phyllotaxy: alternate and spiral (0); alternate and two-ranked (1); opposite and decussate (2); whorled (3)
7.	Leaf succulence: absent (0); present (1)
8.	Stipules: absent (0); present (1)
9.	Stipule structure: not protecting apical bud (0); expanded, surrounding apical bud and leaving a scar on the twig (1)
10.	Axillary buds: with two lateral prophylls (0); with numerous bud scales (1); with no protective scales (2)
11.	Leaf complexity: simple (0); ternately compound (1)
12.	Leaf shape: unlobed (0); lobed or highly dissected (1)
13.	Petiole pulvinus: absent (0); present at base as lower pulvinus (1)
14.	Petiole in cross section: terete to adaxially grooved (0); flattened above, not grooved (1)
15.	Primary and secondary venation: pinnate (0); palmate (1)
16.	Tertiary venation: reticulate (0); percurrent (1)
17.	Leaf margin: crenate to serrate (0); entire (1)
18.	Margin teeth: spinose to rounded, no gland (0); violoid to theoid (1); salicoid (2)
19.	Leaf indumentum: glabrous (0); uni- to multicellular simple hairs (1); glandular hairs (2); stellate hairs (3)
20.	Inflorescence position: axillary (0); terminal (1)
21.	Inflorescence type: monotelic/cymose (0); polytelic/racemose (1)
22.	Inflorescence form: not secund (0); secund with monochasial cymes as subunits (1)
23.	Pedicel: with two bracteoles (0); lacking bracteoles (1); with a single bracteole (2)
24.	Pseudanthium: absent (0); present (1)
25.	Flower symmetry: radial (0); bilateral (1)
26.	Flower sex: perfect (0); imperfect, monoecious or dioecious plants (1)
27.	Hypanthium: absent (0); present (1)
28.	Nectary: present as a disk, often lobed (0); present on or near inner surface of hypanthium (1); absent (2); present as glands opposite each carpel (3); present as staminodial nectaries (4)
29.	Perianth differentiation: sepals and petals (0); tepals (1); perianth absent (2)
30.	Outer perianth whorl: five parts (0); four parts (1)
31.	Petal vs. sepal number: equal (0); petals greater than sepals (1)
32.	Perianth aestivation: sepals and petals valvate (0); sepals and petals imbricate (1); sepals open and petals valvate (2); sepals valvate and petals imbricate (3); sepals imbricate and petals rolled up in bud (4); sepals imbricate and petals open (5)
33.	Outer perianth whorl: at least basally connate (0); distinct (1)
34.	Perianth claws: absent (0); present (1)
35.	Stamen to petal ratio (excluding staminodia): one (0); two or more (1)
36.	Stamen number (excluding staminodia): less than six (0); six or more (1)
37.	Stamen series: haplostemous (0); diplostemous (1)
38.	Stamen insertion: on receptacle (0); on hypanthium or ovary, as a result of adnate hypanthium (1)
39.	Stamen appendages: absent (0); present due to dorsally or apically expanded connective (1)
40.	Staminodia: absent (0); present (1)
41.	Filament:anther length ratio: greater than one (0); less than one (1)
42.	Filament attachment to anther: dorsifixed (0); basifixed (1)
43.	Anther dehiscence: two longitudinal slits (0); valves or flaps (1); one apical slit (2)
44.	Anther dehiscence direction: introrse (0); extrorse (1); latrorse (2)
45.	Number of microsporangia in anther: tetrasporangiate (0); bisporangiate (1)
46.	Filament indumentum: glabrous (0); unicellular, simple hairs (1)
47.	Pollen grain shape: prolate (0); globose (1); oblate (2); bilateral (3)

Table 1. continued

No.	Morphological character and states
48.	Pollen aperture number: three (0); more than three (1); less than three (2)
49.	Pollen aperture distribution and symmetry: triaperturate (0); panaperturate (1); many random pores (2); one pore at each pole of a bilateral grain (3)
50.	Pollen aperture type: colporate (0); colpate (1); porate (2)
51.	Pollen grain ornamentation: punctate (0); smooth/psilate (1); rugulate (2); spinulate, even (3); spinulate, uneven (4); scabrate (5); striate (6)
52.	Tectum organization: punctate (0); continuous (1); interrupted or incomplete (2); reticulate (3)
53.	Aperture membrane: rugose to spinulose (0); smooth (1)
54.	Tectum perforations (hole:ridge ratio): small (0); large (1)
55.	Carpel number: two (0); one (1); five (2); three (3); four (4)
56.	Ovary position: superior (0); inferior (1); partially inferior (2)
57.	Stigma: minute, capitate or punctate (0); decurrent along side of style (1); broad and globose-capitate (2)
58.	Placentation: axile or basal-axile (0); parietal (1); apical-axile (2)
59.	Ovules per locule: two (0); one (1); numerous/more than two (2)
60.	Fruit type: berry (0); nut (1); follicle (2); drupe (3); capsule (4); dry-drupaceous schizocarp (5)
61.	Fruit attachment: to receptacle (0); to gynophore (1)
62.	Persistent styles on fruit: absent (0); present (1)
63.	Winged seeds: absent (0); present (1)

of floral nectaries (char. #28-2, a feature that also characterizes *Haloragis*, *Myriophyllum*, *Penthorum*, and *Tetracarpaea*, while a nectary does occur – possibly representing a reversal – in the Hamamelidaceae, Endress 1989a). Although not included as a formal part of our analysis, sessile flowers are apparently an additional synapomorphy of the woody clade. Most members of the woody clade share anthers opening by valves/flaps (Fig. 3B; char. #43-1), including Hamamelidaceae and *Cercidiphyllum*. Stamen appendages (Fig. 3B; char. 39-1) unite Hamamelidaceae with *Cercidiphyllum* and *Daphniphyllum* (a character also found in the core Saxifragales). The woody clade is united with *Paeonia* L. on the basis of stigmas decurrent along the side of the style (Figs. 3C & 4; char. #57-1), although this stigmatic condition has been lost in *Rhodoleia* (where it is apical, minute and truncate). Hamamelidaceae, represented by *Corylopsis* Sieb. & Zucc., *Hamamelis* L., *Exbucklandia*, and *Rhodoleia*, are united by the apomorphy of stipules expanded and surrounding the apical bud (char. #9-1, but character reversed in *Rhodoleia*) and styles persistent in fruit (Fig. 5A; char. #62-1, under DELTRAN optimization, and occurring also in *Liquidambar* and *Altingia*). Within Hamamelidaceae, stellate hairs unite *Corylopsis* and *Hamamelis* (under DELTRAN optimization, as they also occur in the related *Rhodoleia*), while entire-margined leaves (char. #17-1) are a potential synapomorphy for *Exbucklandia* and *Rhodoleia*. *Cercidiphyllum* and *Daphniphyllum* share imperfect flowers (char. #26-1, a condition also present in *Liquidambar* and *Myriophyllum* and reported to be present in other Hamamelidaceae not sampled here but in Magallón 2007). Bisporangiate anthers (Fig. 3B; char. #45-1) appear to be an autapomorphy of *Hamamelis* and of *Exbucklandia*.

A synapomorphy of Core Saxifragales (i.e., all members of the order except Perdiscaceae and the woody clade + Paeoniaceae – see Endress 1967) is the presence of a hypanthium in their flowers (Fig. 6; char. #27-1, under ACCTRAN optimization) and this feature characterizes all representatives of core Saxifragales included in the analysis except for Crassulaceae. The Saxifragaceae + *Ribes* + *Pterostemon* + Iteaceae clade is supported by the presence of a nectary on the inner surface of the hypanthium (Fig. 7; char. #28-1), while the *Ribes* + Saxifragaceae clade is supported by the lack of a pulvinus (char. #13-1, but very homoplasious, evolving also elsewhere in cladogram, such as in Haloragaceae and relatives) and the petiole merely flattened above (char. #14-1, very homoplasious, also evolving in Hamamelidaceae and relatives, as outlined above). Saxifragaceae, as represented by *Heuchera* L. and *Saxifraga* L., are united by the herbaceous habit with stems rooting at the nodes (chars. #1-1 and 2-1, but very homoplasious, evolving several times in parallel, see Fig. 1),

TABLE 2. Character state codings for Saxifragales: characters 1–33. *See Table 3 for families. **Our interpretation of the showy perianth parts in *Paeonia* is that the outer parts are sepals and the inner parts are petals, which differs from the interpretation of Hiepko (1965).

	Character																															
										1										**2**										**3**			
Genus*	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Liquidambar	0	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	0/1	1	0	1	0	0	1	0	2	2	?	?	?	?
Aphanopetalum	0	1	0	1	0	2	0	1	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	1	0	5	1
Cercidiphyllum	0	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	1	1	0	1	0	2	2	?	?	?	?
Crassula	0	1	0	0	0	2	1	0	?	0	0	0	1	0	0	?	1	?	0	1	0	0	0	0	0	0	0	3	0	0	0	1	0
Kalanchoe	1	1	0	0	0	2	1	0	?	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	3	0	1	0	1	0
Sedum	1	1	0	0	0	0	1	0	?	?	0	0	0	0	0	?	1	?	0	1	0	1	1	0	0	0	0	3	0	1	0	1	1
Daphniphyllum	0	0	0	0	1	0	0	0	?	0	0	0	1	1	0	0	1	?	0	0	1	0	1	0	0	1	0	2	1	1	?	1	0
Ribes	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1/2	0	1	0	2	0	0	0	1	1	0	0/1	0	1	1
Haloragis	1	1	0	0	0	0	0	0	?	1	0	0	?	?	0	?	0	0	1	0	0	0	0	0	0	0	?	2	0	1	0	3	1
Myriophyllum	1	1	0	0	1	3	0	1	0	0	0	1	0	0	0	?	1	?	0	1	1	0	0	0	0	1	?	2	0	1	0	3	1
Corylopsis	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0/1	0	1	3	0	1	0	0	0	0	0	1	0	0	0	0	1	1
Exbucklandia	0	0	0	0	0	1	0	1	1	2	0	1	1	1	1	0	1	?	1	0	?	0	1	0	0	0	?	0	2	?	?	?	?
Hamamelis	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	1	0	0	3	0	1	0	0	0	0	0	0	4	0	1	0	4	1
Rhodoleia	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	?	3	0	1	0	1	1	1	0	0	0	0	?	?	1	0
Choristylis	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0/2	0	0	0	1	1	0	0	0	2	1
Pterostemon	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1/2	1	0	0	1	0	0	0	1	1	0	0	0	3	1
Paeonia	1	1	2	0	1	0	0	0	?	?	1	1	0	0	1	0	1	?	0	1	0	0	1	0	0	0	0	0	0	0	1**	1	1
Penthorum	1	1	2	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	2	0/1	0	1	1	0	0	0	1	2	0	0	?	?	1
Peridiscus	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	?	0	0	1	0	1	0	0	0	0	0	1	1	?	1	1
Heuchera	1	1	0	0	0	0	0	1	0	?	0	1	0	1	1	0	0	1	2	1	0/1	0	0	0	0	0	1	1	0	0	0	1	0
Saxifraga	1	1	0	0	0	0	0	0	?	2	0	0	0	1	0	0	0	1	2	1	0	0	1	0	0	0	1	1	0	0	0	1	0
Tetracarpaea	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	1	0	1	1	0	1	0	0	0	?	2	0	1	0	1	1
Itea	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	2	1
Leea	0	0	0	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Vitis	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0/1	0	0	0	0	0	2	0

Table 2. continued. Character state codings for Saxifragales: characters 34–63. *See Table 3 for families.

	Character																													
	3						**4**										**5**										**6**			
Genus*	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Liquidambar	?	?	0	0	0	0	0	0	1	0	2	0	0	1	1	1	2	0/4	0	0	0	0	2	1	0	2	4	0	1	1
Aphanopetalum	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6	2	0	0	4	2	0	0	1	1	0	0	0
Cercidiphyllum	?	?	1	0	0	1	0	0	1	1	2	0	0	0	0	0	1	5	2	0	0	1	0	1	1	2	2	0	0	0
Crassula	0	0	0	0	0	0	0	0	1	0	2	0	0	2	0	0	0	6	2	0	0	2	0	0	1	2	2	0	0	0
Kalanchoe	0	1	1	0	0	0	0	0	1	0	2	0	0	2	0	0	0	6	2	0	0	4	0	0	1	2	2	0	0	0
Sedum	0	1	1	1	0	0	0	0	1	0	2	0	0	0	0	0	0	6	2	1	0	4	0	0	1	2	2	0	0	0
Daphniphyllum	0	1	1	0	0	1	0	1	1	0	0	0	0	2	0	0	0	2	0	0	0	0	0	1	2	0	3	0	0	0
Ribes	0	0	0	0	1	0	0	0	0	0	0	0	0	0/1	1	1	0	1	1	0	?	0	1	0	1	2	0	0	0	0
Haloragis	0	1	1	0	1	0	0	1	1	0	2	0	0	1/2	1	1	?	4	1	?	?	4	1	2	2	1	1	0	0	0
Myriophyllum	0	1	1	0	1	0	0	1	1	0	2	0	0	2	?	?	2	4	1	1	?	4	1	2	2	1	5	0	0	0
Corylopsis	1	0	0	0	1	1	1	0	1	1	2	0	0	0	0	0	1	1	3	0	0	0	2	1	2	1	4	0	1	0
Exbucklandia	?	?	1	0	1	1	1	0	1	1	1	1	0	1/2	0	0	1	1	3	0	1	0	2	1	2	2	4	0	1	0
Hamamelis	0	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	1	3	0	1	0	2	1	2	1	4	0	1	0
Rhodoleia	0	1	1	0	1	1	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	2	2	4	0	1	0
Choristylis	0	0	0	0	1	1	0	0	0	0	0	0	1	3	2	3	2	2	1	1	?	0	2	2	0	2	4	0	0	0
Pterostemon	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	2	1	0	?	2	2	2	0	2	4	0	0	0
Paeonia	0	1	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	4	0	0	0	0/3/4	0	1	1	2	2	0	0	0
Penthorum	1	1	1	0	1	0	0	0	1	0	2	0	0	0	0	0	0	6	0	0	0	2	2	0	1	2	4	0	0	0
Peridiscus	0	1	1	0	0	0	0	0	1	2	0	0	0	0	0	0	0	4	3	0	0	3	1	0	2	2	3	0	0	0
Heuchera	0	1	1	0	1	0	0	0	1	0	2	0	0	2	0	0	0	0	0	0	0	0	2	0	1	2	2/4	0	1	0
Saxifraga	0	1	1	1	1	0	0	0	1	0	2	0	0	1/2	0	0	0	0	0	0	0	0	2	0	1	2	2	0	1	0
Tetracarpaea	1	0/1	0/1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	2	1	0	?	4	0	0	1	2	2	1	0	0
Itea	0	0	0	0	1	1	0	0	0	0	0	0	1	3	2	3	2	1	0	1	0	0	0	2	0	2	4	0	0	0
Leea	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0/3	0	0	0	0	0	0	0	0
Vitis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

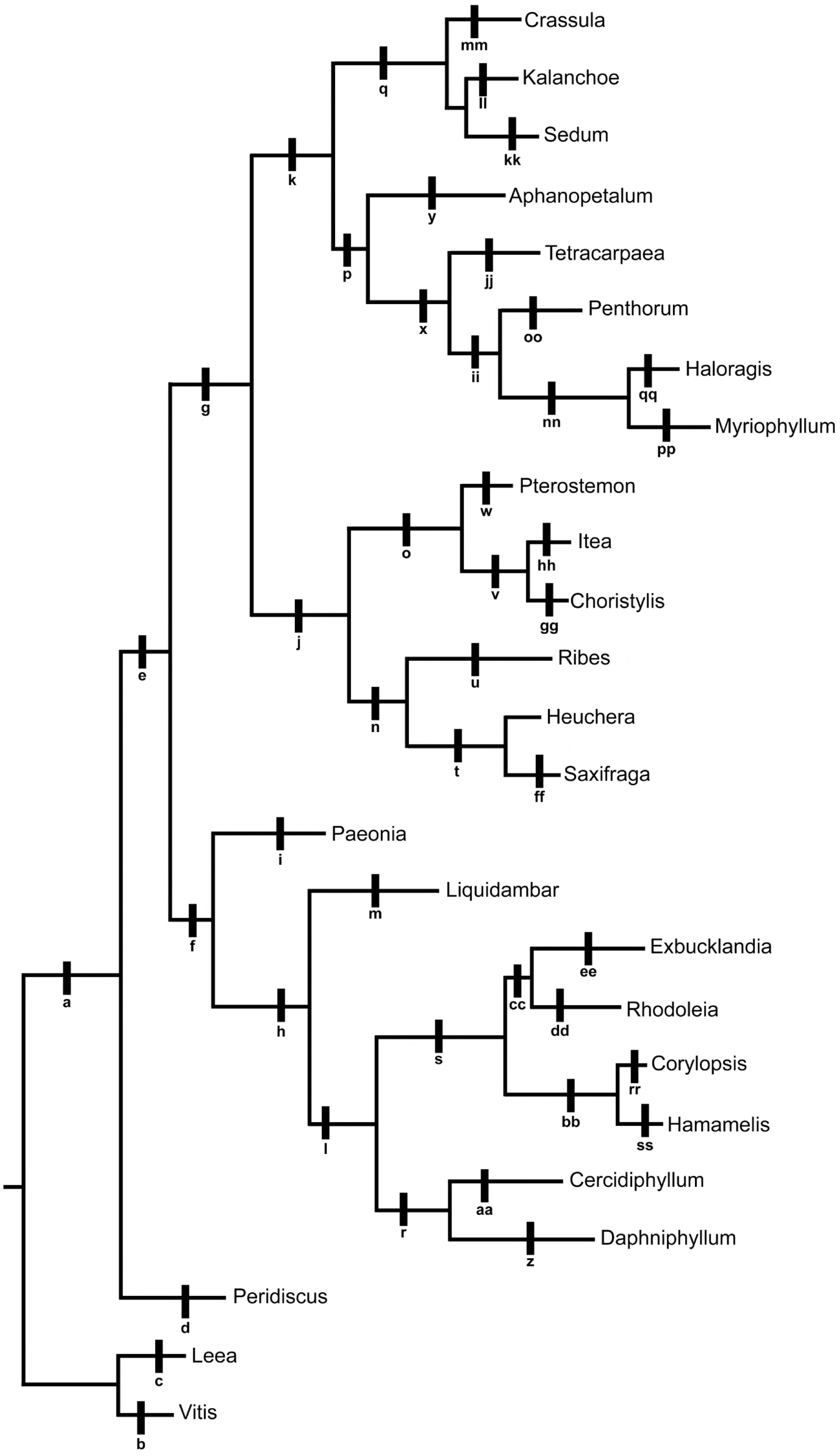

Fig. 1. Morphological characters mapped onto the molecular topology of Jian et al. (2008) using ACCTRAN optimization. Numbers preceding dash are character number, and numbers after dash are state changes (Table 1). a = 18-1, 30-1, 32-1, 33-1, 35-1, 36-1, 42-1, 51-3, 59-2; b = 6-1, 12-1, 13-0, 19-1, 32-2; c = 8-0, 11-1, 15-0, 20-1, 23-0, 40-1, 47-1; d = 9-1, 17-1, 21-1, 29-1, 43-2, 52-3, 55-3, 56-1, 58-2, 60-3; e = 20-1, 44-2, 56-2, 58-1, 60-2; f = 12-1, 57-1; g = 15-0, 23-0, 27-1, 38-1; h = 14-1, 19-1, 20-0, 21-1, 26-1, 28-2, 29-2, 33-0, 60-4, 62-1; i = 1-1, 2-1, 3-2, 5-1, 8-0, 11-1, 13-0, 17-1, 31-1, 56-0; j = 28-1, 35-0, 36-0, 42-0, 44-0, 52-1; k = 2-1, 6-2, 8-0, 51-6, 52-2, 55-4; l = 6-1, 12-0, 15-0, 39-1, 43-1, 58-2; m = 4-1, 10-1, 36-0, 47-1, 48-1, 49-1, 50-2, 58-0, 63-1; n = 12-1, 13-0, 14-1, 15-1, 19-2; o = 19-1, 39-1, 46-1, 51-2, 57-2, 58-0, 60-4; p = 60-1; q = 7-1, 17-1, 27-0, 28-3, 33-0, 38-0, 47-2, 56-0; r = 56-0, 62-0; s = 9-1, 19-3, 26-0, 29-0, 38-1, 40-1, 51-1, 52-3; t = 1-1, 2-1, 10-2, 33-0, 35-1, 36-1, 42-1, 44-2, 47-2, 51-0, 52-0, 62-1; u = 3-1, 5-1, 20-0, 21-1, 23-2, 48-1, 49-1, 51-1, 56-1, 60-0; v = 32-2, 47-3, 48-2, 49-2, 50-2, 53-1; w = 23-1, 32-3, 40-1, 55-2; x = 6-0, 13-0, 23-1, 28-2, 34-1, 52-1; y = 4-1, 8-1, 14-1, 18-2, 20-0, 32-5, 44-0, 58-0, 59-1; z = 5-1, 6-0, 8-0, 17-1, 19-0, 29-1, 41-1, 43-0, 44-0, 47-2, 51-2, 59-0; aa = 3-1, 14-0, 15-1, 20-1, 24-1, 50-1, 51-5, 52-2, 55-1, 58-1, 60-2; bb = 16-1, 23-0, 33-1, 35-0, 36-0, 59-1; cc = 17-1; dd = 6-0, 9-0, 24-1, 25-1, 40-0, 51-0, 52-0, 57-0; ee = 10-2, 12-1, 15-1, 19-1, 29-2, 44-1, 45-1, 47-1/2, 50-1, 54-1; ff = 8-0, 12-0, 15-0, 23-1, 37-1; gg = 14-1, 20-0; hh = 18-0, 21-1, 51-1, 52-0, 56-0; ii = 1-1, 18-0, 32-3; jj = 2-0, 21-1, 38-0, 51-2, 56-0, 60-2, 61-1; kk = 6-0, 13-0, 22-1, 23-1, 33-1, 37-1, 53-1; ll = 14-1, 17-0; mm = 35-0, 36-0, 55-2; nn = 23-0, 34-0, 41-1, 47-2, 48-1, 49-1, 50-2, 51-3, 53-1, 56-1, 57-2, 58-2, 59-1; oo = 3-2, 19-2, 22-1, 30-0, 52-0, 55-2, 60-4; pp = 5-1, 6-3, 8-1, 12-1, 17-1, 21-1, 26-1, 60-5; qq = 10-1, 19-1, 20-0; rr = 27-1, 30-0, 34-1, 50-1; ss = 18-0, 28-4, 32-4, 44-0, 45-1, 54-1.

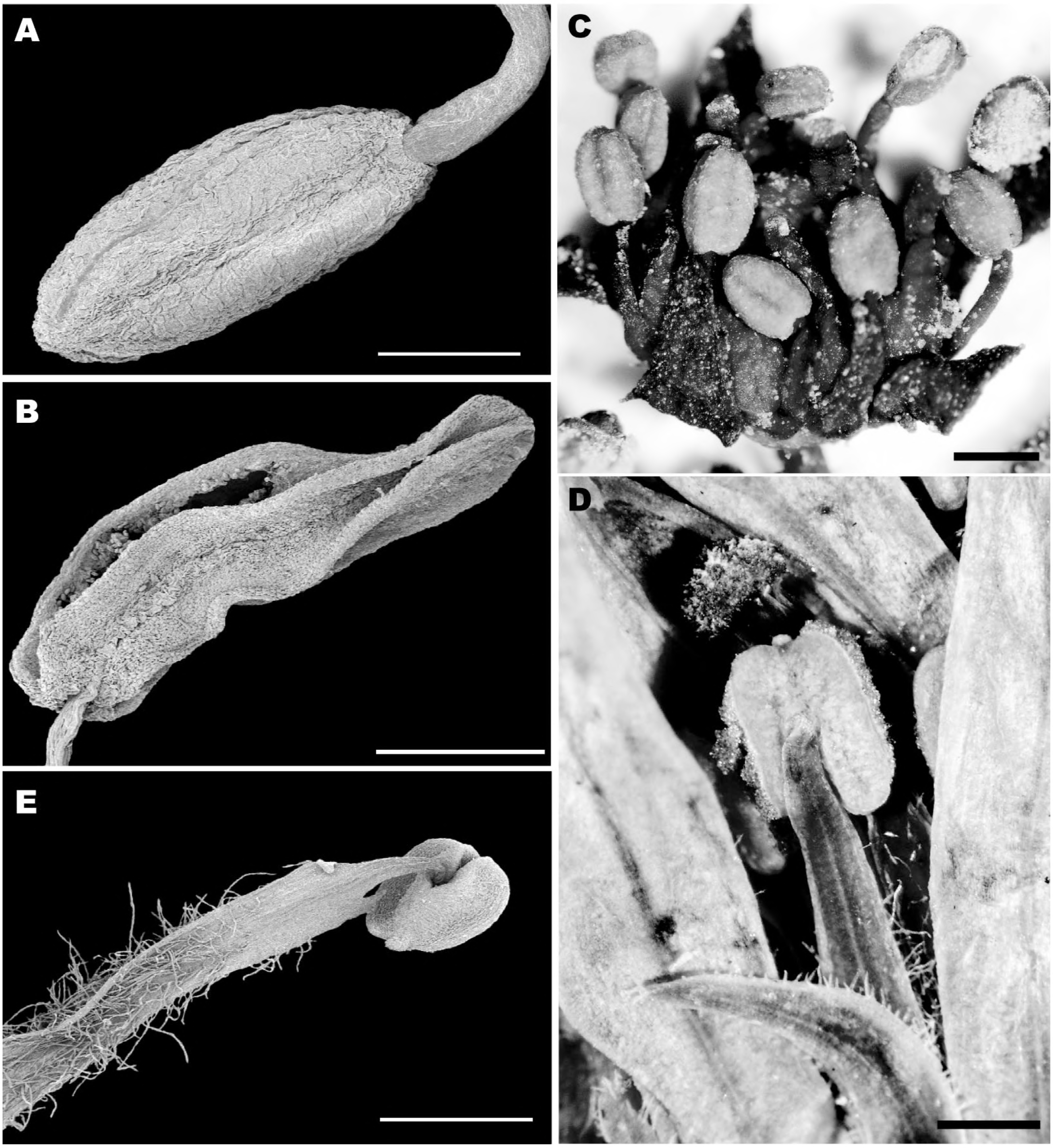

Fig. 2. Synapomorphies for Saxifragales. A–C. Stamens showing basifixed anther (char. #42-1) with filament attached at a basal pit. A. *Tetracarpaea tasmanica* closed stamen, scale bar = 300 µm. B. Open stamen of *Paeonia lactiflora* also showing latrorse dehiscence (char. #44-2), scale bar = 857 µm. C. Androecium of *Penthorum sedoides* with open and closed stamens, scale bar = 500 µm. D-E. Stamens showing dorsifixed condition (char. #42-0). D. Open *Itea virginiana* stamen (foreground) showing unicellular, simple filament hairs (char. #46-1), apically expanded connective (char. #39-1), and (background) globose-capitate stigma (char. #57-2), scale bar = 500 µm. E. Open stamen of *Pterostemon rotundifolius* showing stamen appendage formed from apically expanded connective (pointing down, char. #39-1) and unicellular, simple filament hairs (char. #46-1), scale bar = 1.0 mm.

the outer perianth whorl slightly connate (char. #33-0, but also occurring in *Daphniphyllum*, *Rhodoleia*, *Kalanchoe*, and *Crassula* L.), and oblate pollen grains (char. #47-2, but also occurring in *Daphniphyllum*, *Crassula*, *Kalanchoe*, and Haloragaceae). The *Pterostemon* + *Itea* + *Choristylis* clade is supported by the presence of stamen appendages (Fig. 2D–E; char. #39-1), which develop from the anther connective, but appendages have also evolved in *Cercidiphyllum, Daphniphyllum*, and Hamamelidaceae, and by staminal fila-

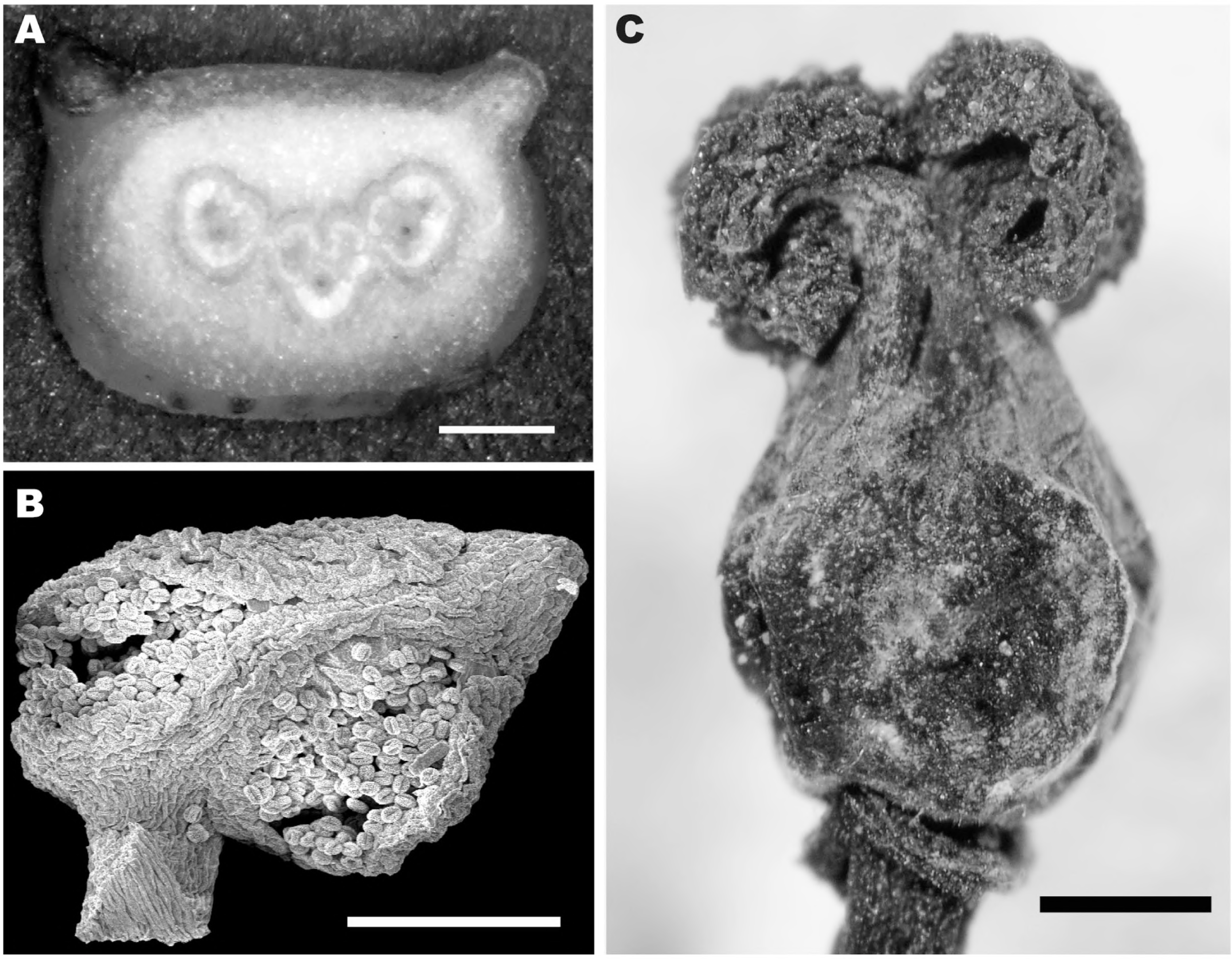

Fig. 3. Synapomorphies for the woody clade and its subclades. A. *Liquidambar styraciflua* petiole transection showing flattened upper surface (char. #14-1), scale bar = 1.0 mm. B. Partially open stamen of *Exbucklandia populnea* showing flaps (char. #43-1) and short apical stamen appendage (char. #39-1, synapomorphy for Hamamelidaceae + *Cercidiphyllum* + *Daphyniphyllum*), scale bar = 200 µm. C. Decurrent stigma of *Daphniphyllum calycinum* (char. #57-1), scale bar = 500 µm.

ments with unicellular hairs (Fig. 2D–E; char. #46-1); other possible synapomorphies of this clade are the capsular fruits (char. #60-4) and expanded, capitate stigmas (Fig. 2D; char. #57-2). Iteaceae (represented by *Itea* and *Choristylis*; probably better treated as a single genus; see Kubitzki, 2007b) share the following putative apomorphies: simple hairs (char. #19-1, under DELTRAN optimization, but quite homoplasious, evolving also in *Haloragis*, *Cercidiphyllum*, *Liquidambar*, and *Exbucklandia*), flowers with open sepals and valvate petals (char. #32-2), and distinctive pollen grains that are bilateral, with only two apertures, one at each pole, with smooth aperture membranes (Fig. 8A; chars. #46-1, 47-1, 48-1, 49-1, 53-1). A putative synapomorphy of the Crassulaceae + *Aphanopetalum* + *Tetracarpaea* + *Penthorum* + Haloragaceae clade is the lack of stipules (char. #8-1, but only under ACCTRAN optimization, and with reversals in *Myriophyllum* and *Aphanopetalum*); but we note that stipules have been lost in parallel elsewhere in the cladogram. Other possible synapomorphies of this large and diverse group are striate pollen (Fig. 8B; char. #51-5, although the pollen of *Tetracarpaea* is smooth, and that of *Haloragis* and *Myriophyllum* spinulate), four carpels (char. #55-4, although both *Penthorum* and *Crassula* have five-carpellate flowers), and the stem frequently rooting at the nodes (char. #2-1, quite homoplasious; see Fig. 1). Crassulaceae are well supported as monophyletic by their succulent leaves (char. #7-1) and the presence of a nectar gland opposite each carpel (Figs. 7 & 8C; char. #28-3). The *Tetracarpaea* + *Penthorum* + *Myriophyllum* + *Haloragis* clade (i.e., Haloragaceae along with closely related families Penthoraceae and Tetracarpaeaceae, although some have suggested that these three

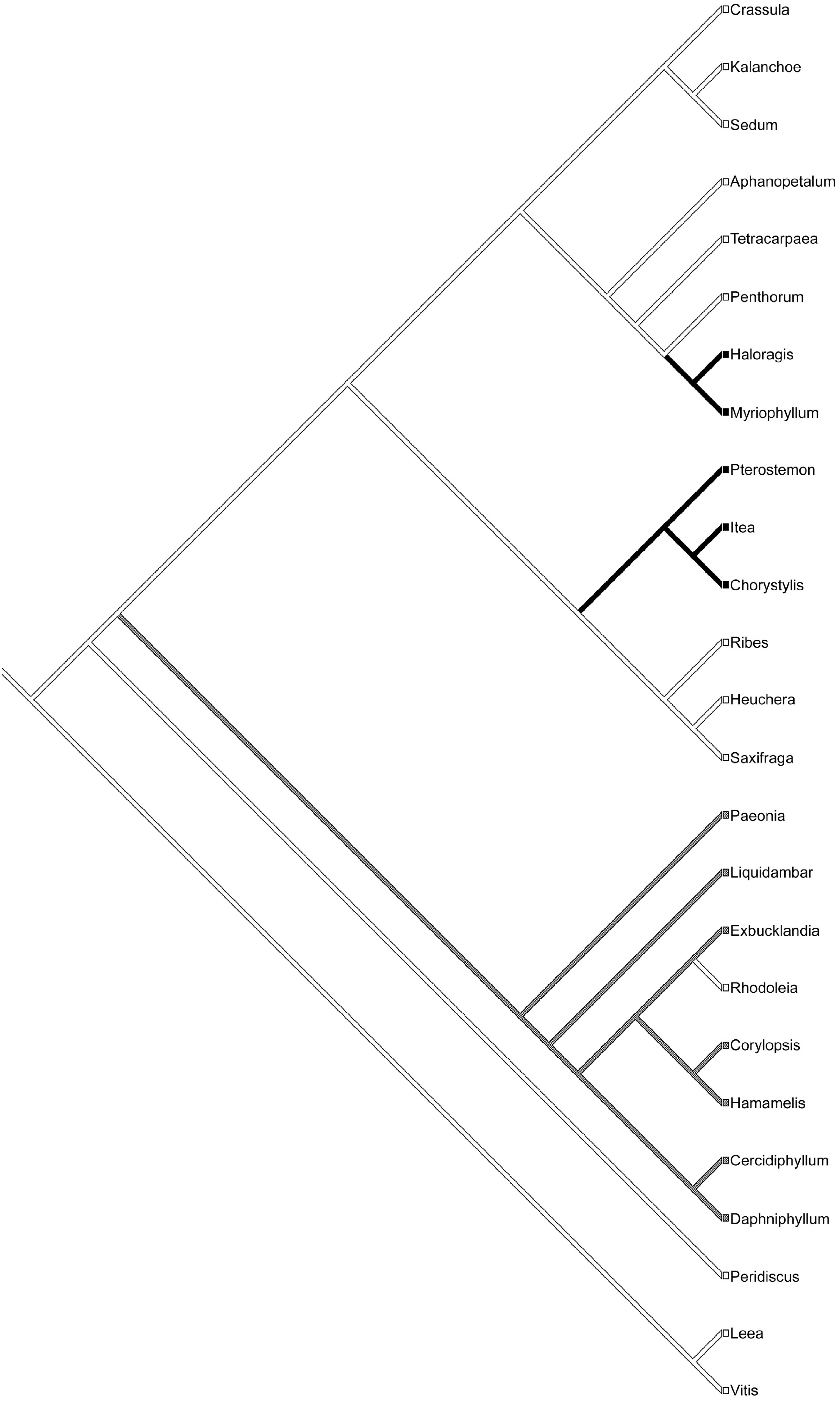

Fig. 4. Character state reconstruction for stigmatic form (char. #57). Lines in white are the plesiomorphic state of a minute, capitate or punctate stigma (char. #57, state 0); grey lines represent stigmas decurrent along side of style (char. #57, state 1; see Fig. 3C); and black lines represent char. #57, state 2, a broad and globose-capitate stigma (see Fig. 2D).

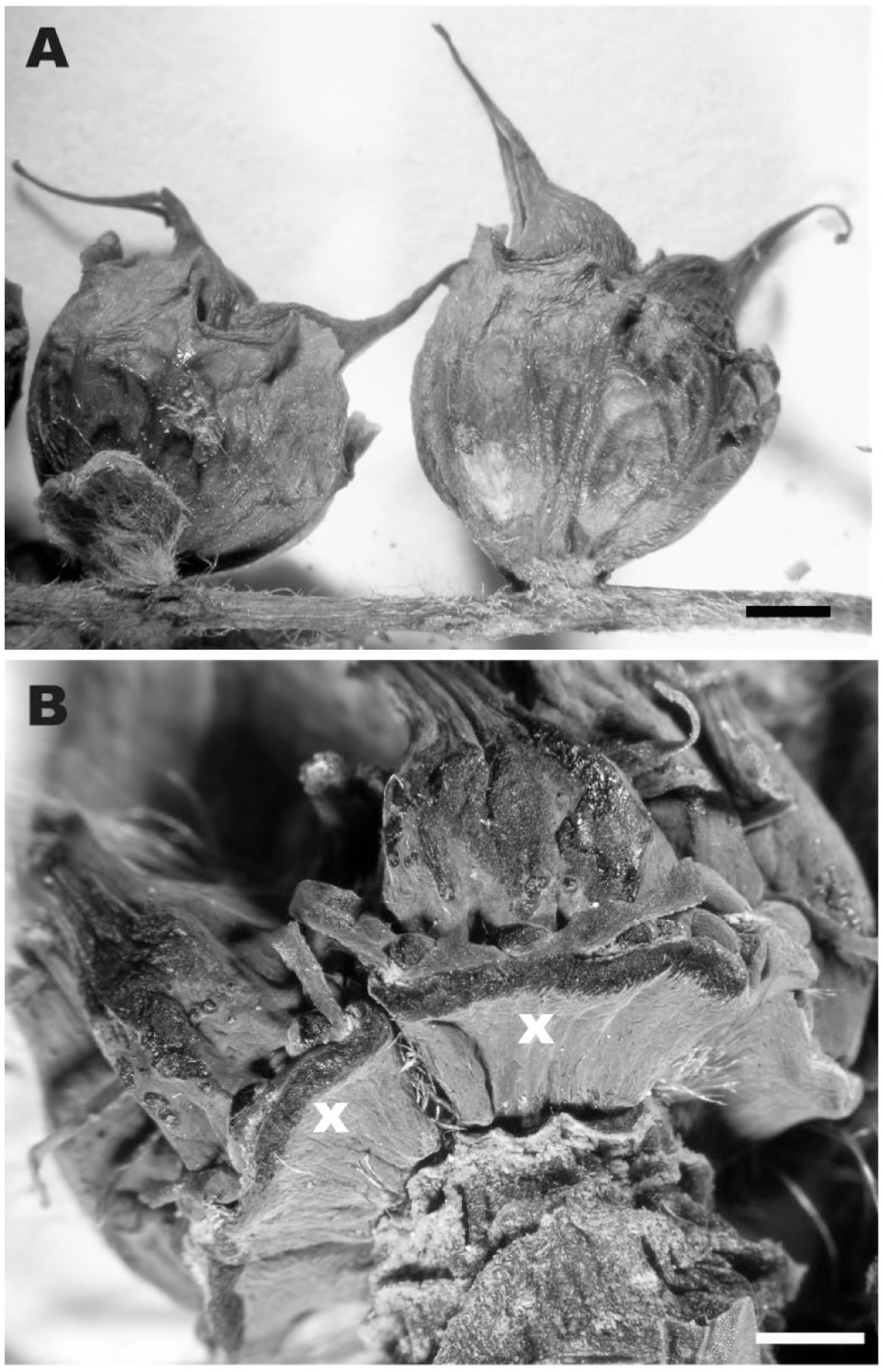

Fig. 5. Characters for Hamamelidaceae. A. Fruits of *Corylopsis paucifolia* showing persistent styles (char. #62-1), scale bar = 1.5 mm. B. Flower of *Rhodoleia championii* showing nectar disk (char. #28-1), scale bar = 1.0 mm.

families could be combined into Haloragaceae s.l.; see Soltis et al. 2005, Jian et al. 2008) are supported by the lack of a pulvinus (char. #13-0) and the absence of nectaries (char. #28-2), but these characters are quite homoplasious. The *Penthorum* + *Myriophyllum* + *Haloragis* clade is supported by the herbaceous habit (char. #1-1) and nonglandular teeth (char. #18-0), while Haloragaceae, as represented by *Myriophyllum* and *Haloragis*, are united by their short filaments in relation to the anther length (Fig. 8D; char. #41-1), spinulose pollen (Figs. 6 & 8E; char. #51-3), globose-capitate stigma (char. #57-2), apical-axile placentation (char. #58-2), and single ovule/locule (char. #59-1).

DISCUSSION

We have identified potential morphological synapomorphies for Saxifragales, including basifixed anthers, often with the filament attached at a basal pit, and violoid to theoid leaf teeth. Stevens (2001) also has suggested that basifixed anthers with a basal pit represent a synapomorphy for members of Saxifragales, however, Endress (1989b; Endress & Stumpf 1991) has noted basal pits only in *Aphanopetalum*, Saxifragaceae, and Crassulaceae. Although chemical, seed-anatomical, and micromorphological characters were outside the scope of our investigation, Stevens also notes the following as potentially apomorphic of the order: presence of ellagic acid, myricetin, flavonols, epicuticular waxes as clustered tubules, and more or less exotestal seeds. He considers the presence of free carpels, or at least apically free carpels, as an ordinal synapomorphy, but our analysis placed this character as a synapomorphy for the clade containing all members of the order

Fig. 6. Character 27, hypanthium presence. A. ***Pterostemon rotundifolius*** **flower longitudinal section showing hypanthium characteristic of the Core Saxifragales, scale bar = 1.5 mm. B. State reconstruction for hypanthium presence (char. #27). Lines in white represent flowers with no hypanthium (state 0), and black lines represent the presence of a hypanthium (state 1).**

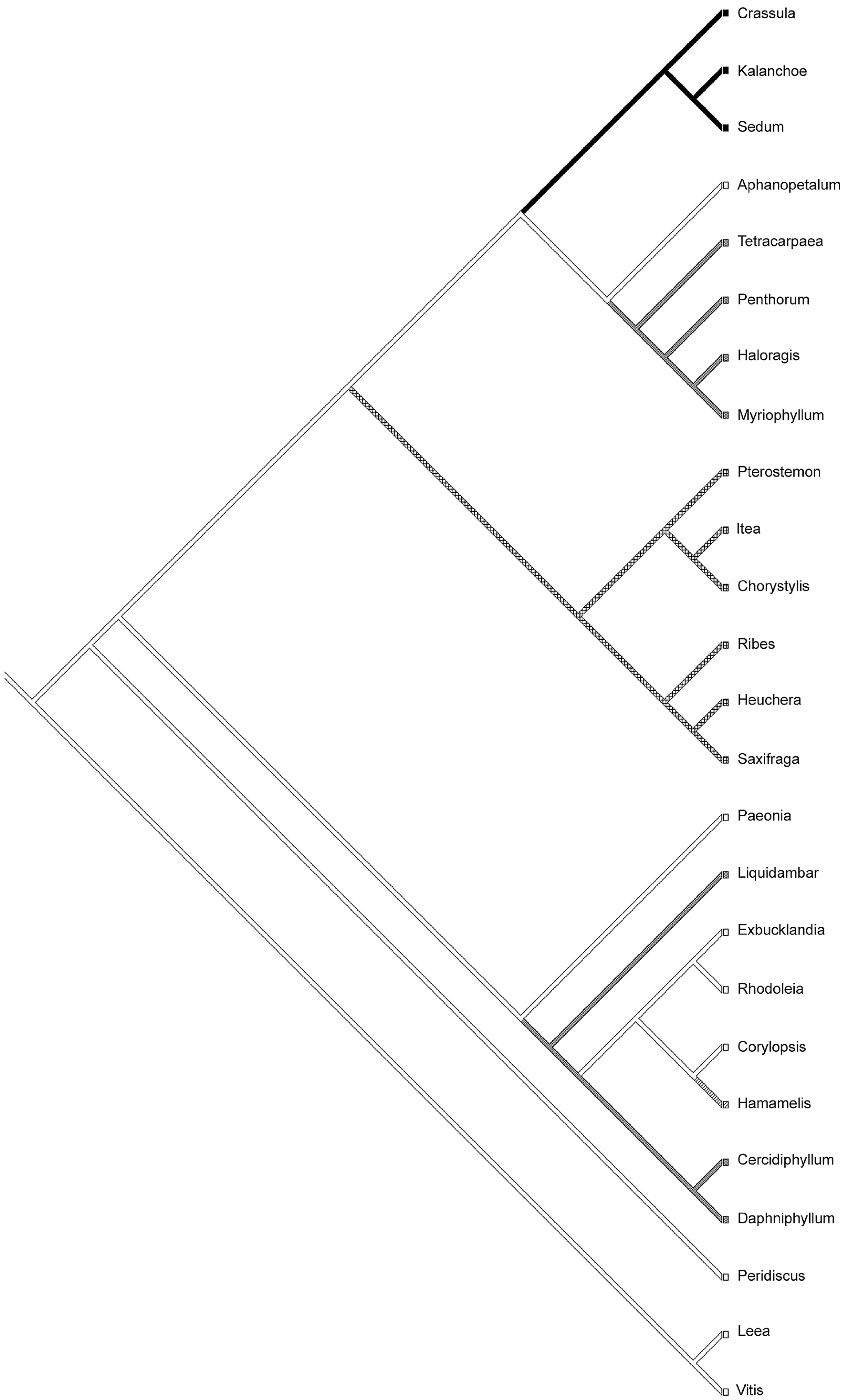

Fig. 7. Character state reconstruction for nectary presence and form (char. #28). White lines represent the plesiomorphic state of nectaries present as a disk (state 0); hatched lines represent nectaries present on or near inner surface of hypanthium (state 1); grey lines represent a loss of nectaries (state 2); black lines represent nectaries present as glands opposite each carpel, pictured in Fig. 8C (state 3); and the striped line represents staminodial nectaries (state 4).

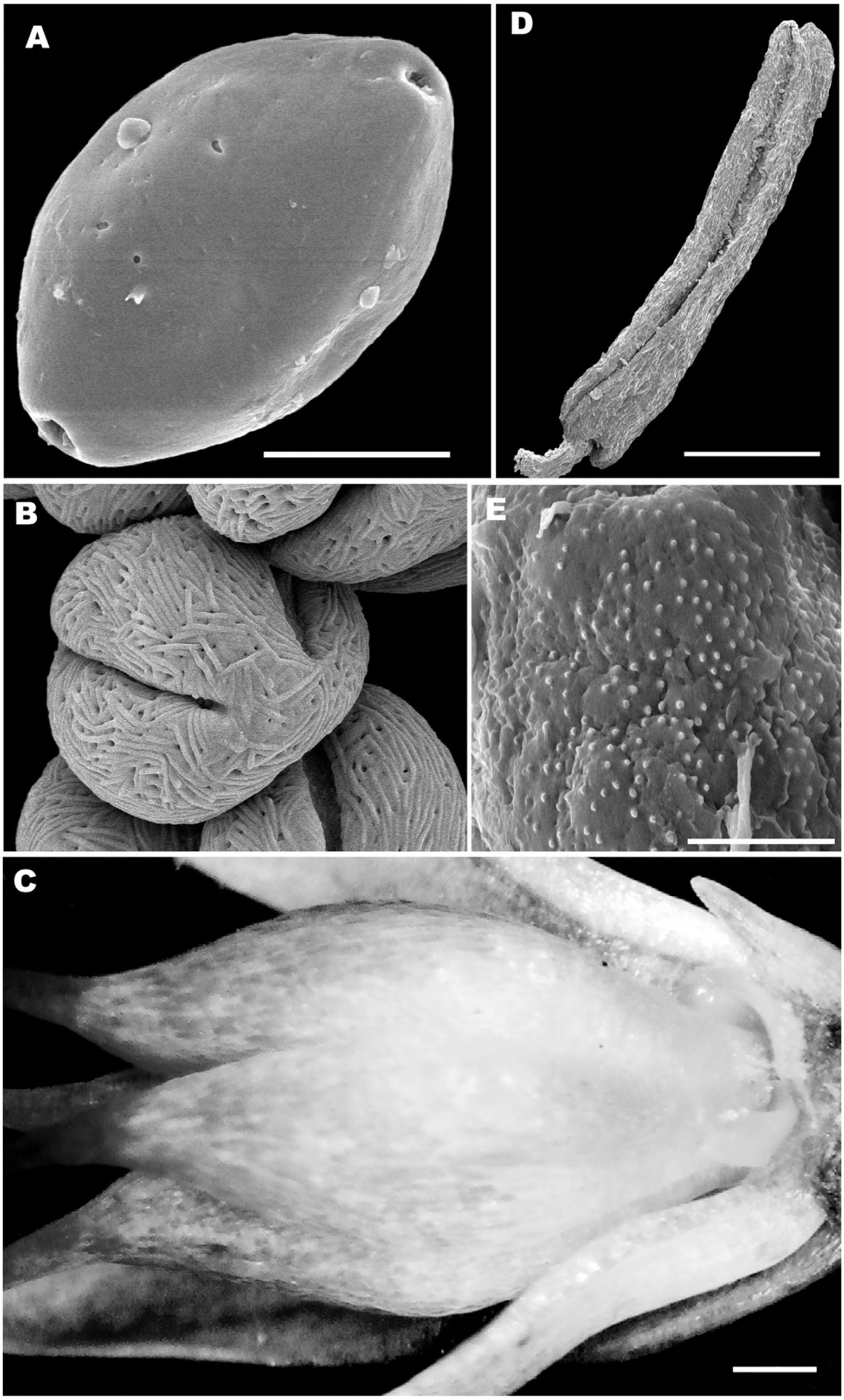

Fig. 8. Synapomorphies for Core Saxifragales, Crassulaceae, and Haloragaceae. A. ***Itea virginiana*** **pollen showing bilateral grains with two apertures and smooth aperture membranes (chars. #46-1, 47-1, 48-1, 49-1, 53-1), scale bar = 7.5 µm. B.** ***Penthorum sedoides*** **pollen showing striate wall (char. #51-5), scale bar = 4.29 µm. C.** ***Crassula*** **flower showing nectar glands opposite each carpel (char. #28-3), scale bar = 1 mm. D–E, Synapomorphies of Haloragaceae. D.** ***Haloragis aspera*** **stamen showing short filaments relative to anther length (char. #41-1), scale bar = 231 µm. E. Close up of exine showing spinulose pattern, in pollen grains of** ***Myriophyllum exalbescens*** **(char. #51-3), scale bar = 3.0 µm.**

except Peridiscaceae. Kubitzki (2007a, p. 17) also considered apocarpy derived in Saxifragales, stating that "it is difficult to imagine that this character expression should be plesiomorphic in these groups."

Our analyses also elucidate character evolution within the clade, a topic briefly addressed by Soltis et al. (2005), although their selection of taxa, cladogram topology, as well as characters considered differed somewhat from ours. Comparisons with our results, therefore, are limited. They hypothesized an ancestral bicarpellate condition in Saxifragales and suggested that only two increases in carpel number have occurred, while our data suggest one increase: in the common ancestor of the Crassulaceae + Haloragaceae + *Aphnopetalum* + *Tetracarpaea* + *Penthorum* clade. Hufford and Endress (1989) suggested that valvate anther dehiscence is plesiomorphic at the level of Hamamelidaceae. Our analysis supports this conclusion, while Soltis et al. (2005) suggested that valvate anthers evolved within the Hamamelidaceae. While our analyses only found imperfect flowers in the clade formed by *Cercidiphyllum* and *Daphniphyllum*, there are representatives of Hamamelidaceae reported with this condition as well (Endress & Igersheim 1999; Magallón 2007).

It is of interest that Hermsen et al. (2006, p. 141), who included 44 morphological characters (several similar to ours) in a phylogenetic analysis of Saxifragales, reported that the Saxifragales "as well as most major infraordinal clades lack unambiguous morphological synapomorphies," however, we note that even homoplasious synapomorphies can be informative. Hermsen and associates included no figures in which morphological characters were mapped onto their tree topologies, but they did mention a few synapomorphies for infraordinal clades, i.e., the presence of a hypanthial nectary in the Saxifragaceae + *Ribes* + *Pterostemon* + Iteaceae clade (Fig. 7; our character #28-1), and the presence of sessile flowers and palmate venation in the Hamamelidaceae + *Liquidambar* + *Cercidiphyllum* clade. We note that their tree topology differed from ours in that *Daphniphyllum* was placed outside this clade. Their hypothesized synapomorphies are in agreement with ours, except that we interpret palmate venation as a retained ancestral character in these taxa. Finally, their results agree with ours in hypothesizing 2-aperturate and porate pollen as synapomorphies for the *Itea* + *Choristylis* clade (i.e., Iteaceae).

Not surprisingly, given the confused taxonomic history of Saxifragales, and reconstruction of phylogeny relying exclusively on molecular characters, clear morphological synapomorphies for major subclades within the order are few. Nonetheless we did discover likely synapomorphies for both the woody clade and Core Saxifragales, as circumscribed in Jian et al. (2008) and Soltis and associates (2011), as well as less inclusive groupings. As might be expected, clades traditionally recognized at familial rank, and represented by more than one taxon in this analysis, usually possess unambiguous shared apomorphies, and these match traditional diagnostic characters, e.g., capsules with persistent styles in Hamamelidaceae, the succulent leaves and distinctive nectar glands of Crassulaceae, the stamens with short filaments, spinulose pollen, and distinctive gynoecium of the flowers of Haloragaceae, or the unusual pollen of Iteaceae. Importantly, phylogenetically useful morphological characters occur across all plant parts (e.g., vegetative morphology, floral and fruit morphology, pollen structure) and can often be correlated with ecologically important syndromes, such as pollination by animals in clades with capitate stigmas, e.g., in our *Pterostemon* + Iteaceae and in Hamamelidaceae (Endress 1989b) or wind pollination in the woody clade where most members have at best a poorly differentiated perianth and are either completely or at least partly wind pollinated (Endress 2010).

The characteristic of bisporangiate anthers within Hamamelidaceae found in *Exbucklandia* and *Hamamelis* appears to be an autapomorphic feature for each genus, and is thus not homologous. Developmental data from Magallón (2007) show that the loss of sporangia involves the reduction of dorsal sporangia in *Exbucklandia*, while in *Hamamelis* it involves the reduction of ventral ones. Also within Hamamelidaceae, while the species of *Corylopsis* we used (i.e., *C. pauciflora*) was haplostemous, there are diplostemous examples in the genus (Endress 1989a). Endress (1989a) also suggested that *Rhodoleia* is diplostemous, but our observations of *R. championii* suggest that it is haplostemous.

The clade united by basifixed anthers without basal pits that includes Altingiaceae, Daphniphyllaceae, Cercidiphyllaceae, and Hamamelidaceae share a suite of common wood anatomical characters including

TABLE 3. Specimens examined. MO = Missouri Botanical Garden herbarium; FLAS = University of Florida herbarium.

Family	Species	Institution (accession no.)	Collector and collection number
Altingiaceae	*Altingia chinensis* (Champ. ex Benth.) Oliv. ex Hance	MO (5699289)	*S. Liu 288*
Altingiaceae	*Altingia excelsa* Noronha	MO (5789511)	*J. Keenan, U. Tun Aung & R. H. Rule 1407*
Altingiaceae	*Liquidambar styraciflua* L.	FLAS (197607)	*B. Tan 353*
Altingiaceae	*Liquidambar styraciflua*	FLAS (206802)	*C. Edwards 36*
Altingiaceae	*Liquidambar styraciflua*	FLAS (207438)	*S.B. Davis 257*
Aphanopetalaceae	*Aphanopetalum resinosum* Endl.	MO (2687699)	*I.R. Telford 4096*
Cercidiphyllaceae	*Cercidiphyllum japonicum* Siebold & Zucc.	FLAS (147373)	*F.G. Meyer & P.M. Mazzeo 14439*
Cercidiphyllaceae	*Cercidiphyllum japonicum*	MO (4216493)	*S.R. Hill 17005*
Cercidiphyllaceae	*Cercidiphyllum japonicum*	MO (5195863)	*T. Takahashi & M. Myahara 2623*
Cercidiphyllaceae	*Cercidiphyllum japonicum*	MO (5789398)	*S. Tsugaru, G. Murata & T. Takahashi 29017*
Crassulaceae	*Crassula argentea* Thunb.	FLAS (142960)	*K. D. Perkins 594*
Crassulaceae	*Kalanchoe daigremontiana* Raym.-Hamet & H. Perrier	FLAS (10551)	*E. West s.n.*
Crassulaceae	*Kalanchoe daigremontiana*	FLAS (163794)	*C. A. Smith s.n.*
Crassulaceae	*Sedum pulchellum* Michx.	FLAS (115480)	*K.E. Blum 3496*
Crassulaceae	*Sedum pulchellum*	MO (5443699)	*C.F. Reed 12960*
Daphniphyllaceae	*Daphniphyllum calycinum* Benth.	MO (4197733)	*Q. Lu 5237*
Daphniphyllaceae	*Daphniphyllum calycinum*	MO (4550419)	*B. Xiong 1539*
Daphniphyllaceae	*Daphniphyllum calycinum*	MO (4688516)	*M. Li 1085*
Grossulariaceae	*Ribes aureum* Pursh	FLAS (99651)	*D. Demaree 38882*
Grossulariaceae	*Ribes aureum*	FLAS (162217)	*R. Burckhalter 598*
Grossulariaceae	*Ribes speciosum* Pursh	FLAS (141782)	*R. Moran 26637*
Haloragaceae	*Haloragis aspera* Lindl.	MO (3630556)	*A.E. Orchard 311*
Haloragaceae	*Haloragis aspera*	MO (4930365)	*N.N. Donner 9922*
Haloragaceae	*Myriophyllum exalbescens* Fernald	FLAS (18181)	*F. F. Wood s.n.*
Haloragaceae	*Myriophyllum exalbescens*	FLAS (53594)	*G.L. Kirk & D.L. Dutton s.n.*
Hamamelidaceae	*Corylopsis pauciflora* Siebold & Zucc.	MO (4942317)	*S.F. Huang, K.C. Yang & J.M. Hu 5194*
Hamamelidaceae	*Corylopsis pauciflora*	MO (5789490)	*R. Nishimura 738*
Hamamelidaceae	*Exbucklandia populnea* (R. Br. ex Griff.) R. W. Brown	MO (52848)	*A. Henry 11068*
Hamamelidaceae	*Exbucklandia populnea*	MO (4967168)	*L. Averyanov CBL224*
Hamamelidaceae	*Exbucklandia populnea*	MO (5591890)	*L. Averyanov VH6061*
Hamamelidaceae	*Hamamelis virginiana* L.	FLAS (40257)	*L.T. Nieland s.n.*
Hamamelidaceae	*Hamamelis virginiana*	FLAS (144237)	*W.S. Judd 2918*
Hamamelidaceae	*Hamamelis virginiana*	FLAS (207613)	*J.R. Abbott 14093*
Hamamelidaceae	*Rhodoleia championii* Hook. f.	FLAS (83474)	*S. McFadden s.n.*
Hamamelidaceae	*Rhodoleia championii*	FLAS (136656)	*F.G. Meyer & P.M. Mazzeo 14221*
Hamamelidaceae	*Rhodoleia championii*	FLAS (148890)	*S. Zona s.n.*
Iteaceae	*Choristylis rhamnoides* Harv.	MO (1787000)	*N.C. Chase 7819*
Iteaceae	*Choristylis rhamnoides*	MO (5796574)	*O.A. Kibure 713*
Iteaceae	*Itea virginica* L.	FLAS (94173)	*I. L. Wiggins 19758*
Iteaceae	*Itea virginica*	FLAS (172551)	*C. Easley 18*
Iteaceae	*Itea virginica*	FLAS (211015)	*C. Kabat 97*
Paeoniaceae	*Paeonia californica* Nutt.	FLAS (158526)	*K. Curry s.n.*
Paeoniaceae	*Paeonia californica*	FLAS (170945)	*S. Zona 312*
Paeoniaceae	*Paeonia lactiflora* Pall.	FLAS (180293)	*Merrgen 113*
Penthoraceae	*Penthorum sedoides* L.	FLAS (35213)	*E. J. Cummings s.n.*
Penthoraceae	*Penthorum sedoides*	FLAS (76636)	*T. Van Bruggen 848*
Peridiscaceae	*Peridiscus lucidus* Benth.	MO (4658118)	*J. Velazco 1807*
Peridiscaceae	*Peridiscus lucidus*	MO (4968760)	*M. A. D. Souzas & M. J. G. Hopkins 516*

Table 3. continued

Family	Species	Institution (accession no.)	Collector and collection number
Pterostemonaceae	*Pterostemon rotundifolius* Ramírez	MO (3417656)	*D. Nava, F. Nava & F. Castillo 43*
Pterostemonaceae	*Pterostemon rotundifolius*	MO (4028404)	*P. Tenorio 11302*
Saxifragaceae	*Heuchera micrantha* Douglas ex Lindl.	FLAS (71623)	*L.S. Rose 41289*
Saxifragaceae	*Heuchera micrantha*	FLAS (55609)	*S. C. Hood 1040*
Saxifragaceae	*Saxifraga virginiensis* Michx.	FLAS (125070)	*D. Soltis 807*
Saxifragaceae	*Saxifraga virginiensis*	FLAS (129997)	*W.C. Brumbach 51-32*
Tetracarpaeaceae	*Tetracarpaea tasmanica* Hook. f.	MO (2314048)	*D.A. Ratkowsky & A.V. Ratkowsky 21*
Tetracarpaeaceae	*Tetracarpaea tasmanica*	MO (4895512)	*J. Bradford, R. Barnes & K. Bradford 898*
Vitaceae	*Leea coccinea* Bojer	FLAS (188082)	*J.R. Abbott 7323*
Vitaceae	*Leea manillensis* Walp.	FLAS (120160)	*G. Joyner s.n.*
Vitaceae	*Vitis aestivalis* Michx.	FLAS (26062)	*K.W. Loucks 23*
Vitaceae	*Vitis aestivalis*	FLAS (68520)	*E.S. Ford 3980*
Vitaceae	*Vitis aestivalis*	FLAS (154089)	*L.M. Baltzell 7191*
Vitaceae	*Vitis aestivalis*	FLAS (154090)	*L.M. Baltzell 7191*

vessels predominately (>90%) solitary, intervascular pitting opposite to scalariform, perforation plates exclusively scalariform usually with more than 20 bars, fibers non-septate and with distinctly bordered pits, and mostly narrow rays 1–3 seriate (based on information available in the "Inside wood" database and imagery). These features (except for vessels predominately solitary) are also shared with *Peridiscus*. Therefore, none of these wood anatomical features can be considered as synapomorphies of the woody clade. It is noteworthy that vessels with simple perforations characterize most herbaceous members of Saxifragales, apparently as a result of parallel evolutionary events (Kubitski 2007a).

Finally, it is significant that even this comparatively straightforward morphological survey (using characters easily recorded from herbarium specimens) generated useful information, allowing morphological characterization of nearly all clades recovered in molecular analyses. This applies even in a group such as Saxifragales, which likely represent an ancient, rapid diversification and are thus relatively character poor (Jian et al. 2008; Hermsen et al. 2006). We anticipate, therefore, useful results upon completion of a comparable morphological survey across the breadth of our large angiosperm cladogram, as well as comparable analyses of Caryophyllales and the Campanulidae (see Cantino et al. 2007).

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SPIRODELA OLIGORRHIZA (LEMNACEAE) IS THE CORRECT NAME FOR THE LESSER GREATER DUCKWEED

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ABSTRACT

A non-native species of duckweed, *Spirodela oligorrhiza* (Lemnaceae), has in recent years become known as *Spirodela punctata* or as *Landoltia punctata*. It is here shown that the basis for "*punctata*" as applied to the introduced plant is incorrect and the generic name *Landoltia* is inappropriate. A neotype is selected for *Lemna punctata*, basionym of *Spirodela punctata*. It is suggested that a long-standing apparent range discontinuity of *Spirodela* in South America is an artifact of data mismanagement.

RESUMEN

Una especie no-nativa de lenteja de agua, *Spirodela oligorrhiza* (Lemnaceae), en los últimos años se ha conocido como *Spirodela punctata* o *Landoltia punctata*. Se demuestra que la base para "*punctata*" como aplicado a la planta introducida es inexacta y el nombre genérico *Landoltia* es inadecuado. Se selecciona un neotipo para *Lemna punctata*, basiónimo de *Spirodela punctata*. Se sugiere que una antigua discontinuidad de rango aparente de *Spirodela* en Sudamérica es un artefacto de mala administración de datos.

INTRODUCTION

The family Lemnaceae consists of four genera: *Lemna*, *Spirodela*, *Wolffia*, and *Wolffiella*. (A fifth genus, *Landoltia*, has been proposed, and will be discussed here.) All species are diminutive thalloid plantlets, floating or slightly submersed on quiet waters. Each plantlet of *Spirodela* produces several roots, while the genus *Lemna* is characterized by each plantlet producing only a single root. (The two remaining genera, *Wolffia* and *Wolffiella*, are without roots.) *Spirodela*, in turn, is formed of 3 species (or 2, if *Landoltia* is split off): *S. polyrrhiza* (L.) Schleiden, whose name is uncontested; a second, known as either *S. oligorrhiza* (Kurz) Hegelmaier or *S. punctata* (Meyer) Thompson (or *Landoltia punctata* (Meyer) Les & Crawford); and a third, presently known as *S. intermedia* W. Koch.

The original ranges of these three species are largely discrete. As based on an extensive compilation of herbarium records (Landolt 1986), *Spirodela polyrrhiza* occurs throughout much of North America, Europe, and temperate Asia. The second species with the conflicted nomenclature (at times cited here as the "Lesser Greater Duckweed") is common in eastern Australia, southeastern Asia, and throughout the islands of the western Pacific. The third species, *S. intermedia*, is widespread in South America. Each species, by modern records, may have extended its range beyond its historic homeland. The most notable—and best recorded—range extension is the introduction of the Australia/Pacific species into the southeastern United States.

A prefatory justification is in order for the vernacular name "Lesser Greater Duckweed," as used in the above title and following text. In matters of nomenclature, where the scientific name is in dispute, an unambiguous common name has value. Plants of the Lemnaceae have from ancient times been called "duck-weed" or "duck-meal." The most familiar genus of the family, *Lemna*, is now invariably reported as "Duckweed" (the archaic European "duck-meal" having faded into obscurity). Species of the related genus *Spirodela*, although similar in form, are generally larger. So that *Spirodela* may be distinguished from *Lemna*, yet reflect their close kinship, botanists have called the native *S. polyrrhiza* the "Greater Duckweed." The introduced *S. oligorrhiza*—the species to be addressed here—has elsewhere been assigned the common name "Dotted Duckweed" in transliteration of the epithet of a misapplied synonym. Plants of *S. oligorrhiza* are smaller than those of *S. polyrrhiza* (yet larger than *Lemna* spp.). In that this little plant is gaining importance as an

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unwelcome weed and thus is in need of its own distinctive common name—and to show its congeneric relation with its larger relative—"Lesser Greater Duckweed" has been volunteered.

The Lesser Greater Duckweed carries three scientific names. Two of these are within the genus *Spirodela*, and one as the single species of the newly-formed genus *Landoltia*. The present task is to explore the history and legitimacy of these names and to determine which of the proposed names best conforms to the morphology of the plant and to the rules of nomenclature. As a secondary but worthy by-product of this nomenclatural mission, a previously unexplained detail of South American plant distribution will be resolved. The search for these answers will require an examination not only of botanical literature but of a nearly forgotten moment of glory in the American history of scientific exploration.

AN OVERVIEW

The Lesser Greater Duckweed became known to American field botanists—though not by that name—with a report by Albert Saeger (1934) of its discovery in a city park of Kansas City, Missouri. Whether known as *Spirodela oligorrhiza* or *Spirodela punctata*, this species is not native to the Americas (Landolt 1986). Saeger included in his report 15 figures showing the plantlets, roots, stamens, and pollen; his plant was unmistakably the Lesser Greater Duckweed. Prior to Saeger's discovery only the Greater Duckweed, *S. polyrrhiza* (L.) Schleid., was known in North America. Saeger made the identification by consulting the then-standard world monograph, that of Friedrich Hegelmaier (1895). Saeger followed Hegelmaier's nomenclature, and reported the plant as *Spirodela oligorrhiza* (Kurz) Hegelm.

Saeger was familiar with an impressive prior study of North American Lemnaceae by Charles H. Thompson (1898). Thompson, in a supplementary footnote, had reported a South American plant he named *Spirodela punctata* (Meyer) Thompson. Thompson had based his description on a collection made in 1838–1842 by an American expedition to the South Pacific. The specimen label indicated (incorrectly; see below) the material to have been collected at Orange Harbor, Tierra del Fuego. Saeger rejected Thompson's *S. punctata* for his Missouri plant, noting that Thompson's description and accompanying figure did not correspond.

The Lemnaceae were again given serious attention by an Illinois botanist, Edwin H. Daubs, first (1962) by reporting the discovery of *Spirodela oligorrhiza* from a number of additional locations in Florida, Illinois, and Louisiana, then second (1965) with a world monograph. Daubs also rejected Thompson's *S. punctata*; he followed Hegelmaier and Saeger in using *S. oligorrhiza*.

In Europe two centers arose with interest in the Lemnaceae. In the Netherlands, den Hartog and van der Plas (1970) summarized their investigations into taxonomy of the family by a synopsis of all pertinent scientific names with full synonymy; they treated the Lesser Greater Duckweed—though again not by that name—as *Spirodela punctata*. In Switzerland, Elias Landolt conducted an extensive research program covering all aspects of the Lemnaceae, culminating (1986) in two magnificently detailed volumes; he too used *S. punctata*. A recent survey of Florida duckweeds (Ward & Hall 2010) touched lightly on the correct name for this species; in agreement with Saeger (1934) and Daubs (1965), they again employed *S. oligorrhiza*. Whatever its scientific name, the Lesser Greater Duckweed in Florida has reached such abundance that in 2009 it became the first member of the Lemnaceae to be classified as "Invasive Plant, Category II" (Florida Exotic Pest Plant Council 2009).

THE EXPEDITION

The probable source of the specimen which Thompson (1898) identified as *Spirodela punctata* needs determination. This will require an understanding of the itinerary of the venture on which it was obtained, the United States South Pacific Exploring Expedition of 1838–1842. The Expedition was often referred to as the "Wilkes Expedition" in acknowledgment of the contribution to its success of its leader, Capt. Charles Wilkes. In 1838 the young and self-confident United States sent out what was at that time the world's largest "voyage of discovery," consisting of six sailing ships and 346 men, charged with exploring and reporting

on the "Great Southern Ocean." Though now generally forgotten by school-book histories, this episode of American exploration has been well documented (Collins 1912; Haskell 1942; Stanton 1975; Eyde 1986).

The Expedition sailed from Norfolk, Virginia, on 18 August 1838. The ships crossed the Atlantic to Madiera, western Africa, then back to Rio de Janeiro, taking soundings along the way but doing no plant collecting. Continuing south, they rounded Cape Horn (losing one ship), then anchored at Orange Harbor, on the western side of Tierra del Fuego, Chile. Here, the captain permitted the scientific personnel to go ashore, and a number of specimens of plants, animals, and rocks were collected.

Continuing north, the Expedition reached Peru (where a second ship was sent home, with personnel the Captain believed divisive). There was opportunity to climb the lower Andean slopes, permitting more collections than had been possible at previous stops. The ships then turned westward, across the Pacific to Reao in the Tuamotus, Tepoto, Tahiti, and Samoa.

The ships then sailed southward, eventually making a much-contested possible first-sighting of the Antarctic continent. They returned north, to Sydney for refitting and resupplying, to Fiji (where they met a genuine cannibal; a native came aboard, gnawing on a detached head), collecting specimens at each anchorage (the cannibal's lunch was also collected, the neatly cleaned skull carried back to Washington). Then east to the Hawaiian Islands where they had ample time and made numerous collections (the Captain needing three weeks to set up an observatory atop Mauna Loa).

By the spring of 1841 the Expedition reached Puget Sound and Oregon (losing another ship in crossing the Columbia River bar), again with opportunity for collecting. A party was sent south by land, reaching central California (and discovering the renowned pitcher-plant, *Darlingtonia californica*). The Expedition then sailed westward, spending a few days in the Philippines, touching briefly at Singapore, then Capetown, across the Atlantic, and home. They reached New York in June 1842, carrying with them an estimated 10,000 plant specimens.

THE SPECIMEN

The specimens collected by the Wilkes Expedition became the core holdings of the young Smithsonian Institution (whose founding in 1846 was stimulated by the happy near-simultaneous arrival of the valued specimens and an endowment from James Smithson of England). One of these specimens, now cataloged as US 18220, is a packet containing plantlets of a *Spirodela*. An otherwise-blank handwritten label (the hand not identified) reads: "*Lemna*" and "Orange Harbor, Tierra del Fuego." The sheet to which the packet is attached also bears a printed label recording the specimen as being part of the "Herbarium of the U.S. South Pacific Exploring Expedition, under the command of Capt. Wilkes, U.S.N., 1838–42." Data on the printed label is again a simple handwritten "*Lemna*." The sheet bears an annotation by C.H. Thompson as "*Spirodela punctata* (Meyer) Th." and "(*Lemna ? punctata* Meyer)." The sheet was further annotated in 1962 by E.H. Daubs "AS DETERMINED." There is no reason to doubt, having been verified by Thompson and then by Daubs, that the lemnoid in the packet is the Lesser Greater Duckweed, known to Thompson (1898) as *Spirodela punctata* and to Daubs (1965) as *S. oligorrhiza*. (Daubs knew Thompson had treated this as *S. punctata*. It may be that at the time of his annotation in 1962, Daubs had not rejected Thompson's name, as he did by 1965.)

No modern author has disputed Thompson's assertion that *Spirodela* occurs in southern Chile and Argentina. This claim was supported by inclusion of *S. punctata* in *Flora Patagonica* by Maevia N. Correa (1969). Her comments, however, confined it to Orange Harbor, Tierra del Fuego, as described by Thompson (1898), and to the specimen (*US 18220*) collected by the Expedition. [Correa cited a second collection, *Spegazzani 1534* (LP); it has not been traced.] *Spirodela* in Tierra del Fuego is unknown to other collectors (T. R. Dudley [and Natalie Goodall], pers. comm., Oct 1989, Nov 1992). Except for the single Expedition specimen, no collections of *Spirodela* have been mapped for southern South America (Landolt 1986).

If the Expedition collection, labeled as from Tierra del Fuego, were not from that location, what might have been its source? After the Expedition returned to the States the valuable specimens were handled ir-

regularly, even chaotically (Haskell 1942). Since the label is printed, it must have been composed after the Expedition's return. It seems evident that the label became attached to the wrong packet. The itinerary of the Expedition provided many opportunities for collection of the Australia/South Pacific species. The true source of the supposed Tierra del Fuego specimen is most probably eastern Australia or one of the South Pacific islands.

SOUTH AMERICAN RANGE DISJUNCTION

If the Tierra del Fuego specimen was mislabeled, a question raised by Correa (1969) is resolved. She noted *Spirodela punctata* (the name she employed) was known in Central America and northern South America, but was unknown between Guyana, its type locality, and Patagonia. She stated that she was addressing this disjunction in range in a forthcoming article in *Darwiniana*, volume 15. She gave no suggestion as to her explanation and conclusion. But by her death in 2005, no such article had appeared.

Though Correa (1969) did not have access to ranges of the species as detailed by Landolt (1986), her query was insightful. It can now be answered with confidence. The report of *Spirodela* in southern South America, exemplified by the reported Tierra del Fuego specimen, is surely an error. And the apparent disjunction of the species between the tropical climate of Guyana and the frigid South American sub-antarctic is an artifact of simple specimen mishandling, long uncritically accepted.

TYPIFICATION

Spirodela punctata (Meyer) Thompson is a legitimate name (though not necessarily "correct" in a nomenclatural sense; see McNeill et al. 2006). Its basionym, *Lemna punctata* G.F.W. Meyer (1818), is of a specimen from the Essequibo River, Guyana, northern South America. Meyer's collections are largely at GOET. But Meyer's type of *S. punctata* has been lost (Landolt 1986). What that type may have been will determine the correct name of the Lesser Greater Duckweed.

Even without Meyer's Guyana type, there is no difficulty in determining the probable identity of his plant. Only one species of *Spirodela* is native to South America: *S. intermedia* W. Koch (1932). Landolt (1986) has confirmed *S. intermedia* is to be found in the immediate vicinity of the Essequibo River. Moreover, he noted that Meyer's description of *L. punctata* closely resembles young material of *S. intermedia*.

If the plant known to Meyer and named *Lemna punctata* by him is indeed the only species of *Spirodela* to be found in Guyana, and Meyer's description is in accord with local plants, then Meyer's epithet (basionym: 1818) is prior and must be employed. As transferred to *Spirodela*, the native South American plant is correctly identified as *S. punctata* (Meyer) Thompson. The name currently in use for the native species, *S. intermedia* W. Koch, though legitimate, is reduced to synonymy under *S. punctata*.

With *Spirodela punctata* properly assigned to the native South American species, and the non-native North American species understood to be the same as plants from the southern Pacific, identification of the North American introduction is straightforward. The earliest available epithet is *Lemna oligorrhiza* Kurz (1866). Transferred to *Spirodela*, the native Pacific and introduced North American plant is *S. oligorrhiza* (Kurz) Hegelmaier.

THE EXPLANATION

How did things go wrong? How did this single specimen purportedly from Tierra del Fuego cause two-thirds of the species of *Spirodela* to become misnamed?

Thompson (1898), the originator of the belief the *Lemna* (or *Spirodela*) of Meyer's Guyana was the same as the *Spirodela* collected by the Wilkes Expedition, had employed a simple strategem. Since he could not examine Meyer's lost type, he described *S. punctata* from the one specimen to which he had access, the US specimen labeled as from Tierra del Fuego. He appreciated that Guyana and Tierra del Fuego are at opposite ends of the continent. But he reasoned that "many species of the order have even a far wider range," and that "the Fuegian plants answer Meyer's description so admirably in all essential characters." (They do not; see Saeger 1934.)

Saeger (1934) and Daubs (1965), relying on the descriptions and distributions reported by Hegelmaier (1895), rejected Thompson's name for the species they found introduced into the central and southeastern United States. They may have been influenced by Hegelmaier's world-wide monographic coverage, while Thompson was reporting on a single specimen from outside his North American area of expertise.

Landolt, not withstanding his thorough coverage of the biology of the Lemnaceae, did not present himself as a nomenclaturalist. He was aware that *Spirodela punctata* was insecurely typified. He (1986: 439) forthrightly apologized for using Meyer's name: "[T]he identity of *L. punctata* G.F.W. Meyer is not quite sure. The type collection is lost. The description of *L. punctata* can also fit that of poorly developed plants of *S. intermedia*, which occurs near the original type locality (Essequibo River, Guyana)." He even cast doubt on the status of the few South American collections of *S. punctata* cited by him, suggesting that "this loose group was included by mistake." But he moved on, noting that "Thompson retypified the species name of *S. punctata* clearly. His typification has been accepted for a long time."

Landolt's doubts regarding the plant that stood behind Meyer's early name were not given weight by the numerous subsequent writers who, impressed by his overall academic achievement, accepted without question *Spirodela punctata* as the name for the introduced North American species.

Landolt merits praise for his scrupulous detailing of data, even where it encourages reappraisal by other parties. But he erred in stating Thompson "retypified" the species. Thompson's text shows he was describing a specimen he believed to be the same as the type. The modern *International Code of Botanical Nomenclature* (McNeill et al. 2006) permits a later person to select a replacement, a neotype. If Thompson had indicated in any clear way that the specimen he was describing was intended as a replacement for the missing type, his action would be interpreted as neotypification. But he seemed unaware that Meyer's type had been lost. He simply stated, "My description of the species is based on a collection of the plants … made by the United States South Pacific Exploring Expedition."

If neotypification by Thompson were to be put forward, the choice of a plant essentially absent from the continent of its basionym does violence to the concept that a neotype should be as similar as possible to the original type. Since that is not the case (any Guyana specimen of *S. intermedia* would be a more suitable type), invocation of the *Code* (Art. 9.16) would permit the Expedition specimen to be superseded.

A NEOTYPE FOR *SPIRODELA PUNCTATA*

In the belief that the plant from Guyana described by Meyer in 1818 is the same as the plant widespread and native in South America, and to give stability to the nomenclature of this small genus, a neotype is here selected.

Lemna punctata G.F.W. Meyer, Prim. Fl. Esseq. 262. 1818. Type: SURINAM: swamp pool, road to the coast, near Paramaribo, 24 Jan 1951, *J. & P.A. Florschütz 1060* (neotype, selected here: NY). Det. J.C. Lindeman (1951), annot. R.A. DeFilipps (1997), as *Spirodela intermedia* W. Koch. = *Spirodela punctata* (Meyer) Thompson, Rep. Missouri Bot. Gard. 9:28. 1897.

THE GENUS *LANDOLTIA*

The Lesser Greater Duckweed cannot yet rest secure with *Spirodela oligorrhiza* as its scientific name. Modern science, in the form of DNA-based cladistics, has asserted its claim. Les and Crawford (1999) have proposed that *S. oligorrhiza* (their *S. punctata*) be separated at generic rank from its two close relatives, *S. intermedia* and *S. polyrrhiza*.

Spirodela and *Lemna* are morphologically quite similar. Species of *Spirodela* (s.l.) are distinguished from all species of *Lemna* by the presence of several roots per plantlet (vs. a single root). Landolt (1986:464) buttressed this striking difference with others less apparent: *Spirodela* has the "frond surrounded at the base by a small, scale-like leaflet covering the root point of attachment; pigment cells present; crystal cells with either raphides or druses; external locules of the stamen situated at the same level as or somewhat higher than the internal ones," while *Lemna* has "no leaflet at base of the frond covering the point of attachment of the root; no pigment cells (red pigmentation present in some species); raphides but no druses present; the external locules of the stamen situated at the top of the inner ones."

Les and Crawford (1999) employed chloroplast DNA sequences, as well as morphological and allozyme data, to support their contention that *S. oligorrhiza* (= *S. punctata*, *sensu* Les & Crawford) was sufficiently different from the other two species of *Spirodela* as to merit generic ranking. They argued that their re-analysis of *Spirodela* and *Lemna* morphology demonstrated *S. oligorrhiza* (= *S. punctata*, *ibid.*) to fall into a clade between the two recognized genera, and not within either. They stated their allozyme data (part yet unpublished) also supported an intermediate position. They acknowledged, however, that *Spirodela* had not previously been suggested for formation of segregate genera.

Les and Crawford (1999) dismissed the classification employed by Landolt (and others) as being paraphyletic. They considered *S. polyrrhiza* and *S. intermedia* to be sister species, but with *S. oligorrhiza* (= *S. punctata*, *ibid.*) associating with *Lemna*. They provided phylogenetic diagrams of the relationships as inferred by (a) Landolt; (b) themselves, as based on morphology; and (c) their DNA analysis. Each diagram implied a different evolutionary pathway. They chose the third diagram, based on data obtained from the selected segment of chloroplast DNA, as best representing the evolutionary relationships of the Lemnaceae.

With their target species considered closer to *Lemna* than to *Spirodela* (s.s.) and not a member of either, Les and Crawford (1999) believed it appropriate to recognize *S. oligorrhiza* (= *S. punctata*, *ibid.*) as a new genus to better reflect this "revised hypothesis of duckweed relationships." They selected *Landoltia* for its name, in honor of the scholarly work on the family by Elias Landolt.

A response to Les and Crawford (1999) must be made from four directions, some factual and others philosophical. First, of course, as established by selection (above) of a South American neotype for Meyer's Guyana plant, the name *Landoltia* becomes irretrievably attached to the plant presently known as *Spirodela intermedia*, a wholly unwelcome outcome.

Second, the comments by Les and Crawford (1999) regarding morphology are not unchallengeable. As they observed, no previous author has considered dividing *Spirodela* into two genera; even the lesser rank of section has been employed cautiously. Den Hartog and van der Plas (1970: 359) noted that one previous author had distinguished two "species groups" within *Spirodela*; but they stated that, in their opinion, these groups were too insignificant to be regarded even as separate sections. The reason for the failure of previous workers to divide *Spirodela* must in large part rest on the conspicuous morphological character found in all species of the genus—the difference in number of roots on a plantlet. Though less readily observed, other morphological differences described by Landolt (1986), especially the scale-like leaflet surrounding the root base, cannot be matched in *Lemna*.

Third, Les and Crawford's cpDNA conclusions are based on a "hypothesis" (their word), as is of course any analysis that has access to no more that a segment of chloroplast DNA and no nuclear DNA. This is not to fault the technology, but to call attention to the necessarily tentative basis of close DNA-based evolutionary pathways.

And fourth—and perhaps most importantly—heavy reliance on DNA data causes a slighting of characters that can actually be observed in every-day taxonomic work. Verifiable observation becomes secondary to trust in the conclusions of others. If a plant is to be identified in the field, or even under laboratory conditions of magnification, it is important, even vital, that one or more characters be available to permit the determination. Several roots are present, or they are not; a scale is present, or it is not. Once these unifying characters are set aside, classification becomes based upon any number of revisable hypotheses. To split a genus of incontestable morphological similarity, especially one of such small (three-species) size, cannot but confuse those parties whose interest is plant identification. Morphological clarity is lost.

The approach of Les and Crawford (1999) is not to be belittled, for even as a hypothesis their suggested diagram of evolutionary pathways is of informational value. Yet to use that scant basis as justification for nomenclatural change is an unproductive over-extension of their work.

CONCLUSION

The Lesser Greater Duckweed, a species native to Australia and the South Pacific and introduced into eastern

North America, is correctly known as *Spirodela oligorrhiza* (Kurz) Hegelmaier, and the name *Spirodela punctata* (Meyer) Thompson is correctly assigned to a species native to South America and presently known as *Spirodela intermedia* W. Koch. A neotype is selected for *S. punctata*, restricting that name to the South American native. By this neotypification the name *Landoltia* becomes correctly applied to the South American species. Recognition of the segregate genus *Landoltia* is unwise. Reports of *Spirodela* as occurring in far-southern South America are very probably incorrect.

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BOOK REVIEW

Erwin Evert. 2010. **Vascular Plants of the Greater Yellowstone Area: Annotated Catalog and Atlas.** (No ISBN, pbk.). Privately published by the author. (**Orders:** yolandaevert@yahoo.com; 1476 Tyrell Avenue, Park Ridge, Illinois 60068, U.S.A.; also available from MBG Press, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.; 314-57-9594; 314-577-9547 fax). $45.00 (check payable to Yolanda Evert), 751 pp., color relief map, 8½" ×10⅞".

The Rocky Mountains of northwestern Wyoming, southwestern Montana, and eastern Idaho was one of the last areas of the conterminous United States to be settled or thoroughly explored. Rugged terrain, high elevations, and long-lasting snow kept out all but the hardiest indigenous tribes and mountain men well into the 1860s. Today this "Greater Yellowstone Area" (GYA or the Greater Yellowstone Ecosystem) contains the largest extent of high elevation wilderness in the lower 48 states and is a last stronghold for many large and iconic animal species that were mostly extirpated elsewhere in the country. Millions of tourists make the trek to this area annually to enjoy breathtaking mountain scenery, observe wildlife, or have a wilderness adventure.

For all the interest in the ecology of the Greater Yellowstone Area, it is surprising that no definitive floristic synthesis of the region has been produced – at least until now. Erwin Evert's *Vascular Plants of the Greater Yellowstone Area: Annotated Catalog and Atlas* is the first compilation of floristic research from Yellowstone and Grand Teton national parks and the adjacent mountain ranges that comprise the GYA. Evert's tome documents 2,287 vascular plant species and varieties. The treatment is based on Evert's own prodigious field work (>42,000 numbered collections, deposited at the Rocky Mountain Herbarium and the Morton Arboretum) over the past 40 years, as well as a review of thousands of additional collections from regional herbaria. Although technically an "amateur" (a retired science teacher in the Chicago public school system) Evert had a critical eye for novelties and discovered and named four species (*Antennaria aromatica*, *Lomatium attenuatum*, *Penstemon absarokensis*, and the monotypic *Shoshonea pulvinata*) and documented dozens of state records for the flora of Wyoming. A fifth new species, *Cymopterus evertii*, endemic to Wyoming and Utah, was named in his honor.

Evert's catalog begins with an extensive overview of the physiography, climate, vegetation, and biogeography of the greater Yellowstone region. Evert also provides a detailed historical narrative of past botanical research in the region. The meat of the catalog consists of a brief description of the distribution of each plant species within the Greater Yellowstone area (and range-wide), as well as supplemental information on habitat, abundance, conservation status, synonyms, and taxonomic problems. Evert's nomenclature is conservative, mostly following the *Flora of the Pacific Northwest*.

A dot map accompanies each species account and indicates distribution by county and within Yellowstone and Grand Teton national parks. Only one dot is provided per entity to signify confirmed presence (a solid dot) or reported occurrence (open circle) based on literature. The map of Yellowstone National Park needs to be carefully interpreted, as the park actually straddles five counties in all three states, but is portrayed as being its own county-equivalent in northwestern Wyoming.

Erwin Evert's book is a welcome addition to the library of references on the region and a tribute to the important contributions that can be made by "amateur" academics. Sadly, Evert died just a few weeks after his book was published and nearly 20 years after embarking on the project. Evert passed away on his daily botanical foray not far from his beloved cabin on Kitty Creek in the Absaroka Mountains, a few miles east of Yellowstone. Thankfully, his *Annotated Catalog and Atlas* will be his enduring legacy.—*Walter Fertig, Moenave Botanical Consulting, Kanab, Utah 84741 and Ronald L. Hartman, Rocky Mountain Herbarium, 1000 E. University Ave., University of Wyoming, Laramie, Wyoming 82071-3165, U.S.A.*

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THOMAS WALTER'S ORCHIDS

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ABSTRACT

Thomas Walter, author of *Flora Caroliniana* (1788), treated sixteen orchids within the genera *Arethusa*, *Cypripedium*, *Limodorum*, *Ophrys*, and *Orchis* (Orchidaceae). Some of Walter's species have been long recognized. But others have been overlooked in monographic and floristic studies. Walter's names are here associated with the modern species they represent, within the genera *Calopogon*, *Cleistes*, *Cypripedium*, *Hexalectris*, *Platanthera*, *Pogonia*, *Ponthieva*, and *Spiranthes*, as well as perhaps within *Habenaria*, *Isotria*, *Liparis*, or *Triphora*. The argument is made that the orchids appear to provide evidence of a greater collection range for Walter than is usually credited to him. A warning is expressed that the early date of Walter's overlooked names puts a significant number of them, if identified and neotypified, prior to long-accepted modern names.

Key Words: Thomas Walter, Flora Caroliniana, Orchidaceae, *Calopogon, Cleistes, Hexalectris, Platanthera, Pogonia, Ponthieva, Spiranthes*

RESUMEN

Thomas Walter, el autor de *Flora Caroliniana* (1788), examinó dieciséis orquídeas de los géneros *Arethusa*, *Cypripedium*, *Limodorum*, *Ophrys*, y *Orchis* (Orchidaceae). Algunas de las especies de Walter se han reconocido desde hace tiempo. Pero otras se han pasado por alto en estudios monográficos y florísticos. Los nombres de Walter están aquí asociados con las especies modernas que representan, dentro de los géneros *Calopogon*, *Cleistes*, *Cypripedium*, *Hexalectris*, *Platanthera*, *Pogonia*, *Ponthieva*, y *Spiranthes*, así como tal vez dentro de *Habenaria*, *Isotria*, *Liparis*, o *Triphora*. Se argumenta que las orquídeas parecen proporcionar pruebas de un rango de colección por Walter más amplio del que se le admite normalmente. Se expresa una advertencia que la fecha inicial de los nombres de Walter que fueron pasados por alto pone un número significativo de ellos, si se identifican y se neotipifican, antes que los nombres modernos aceptados desde hace tiempo.

Thomas Walter, owner of a rice plantation on the Santee River, Berkeley County, South Carolina, was also the author of a small book, *Flora Caroliniana* (1788), in which he described the plants of his region. The early date of this publication has given Walter's many new names priority over later names, and the author designation "Walt." is familiar to all students of the Coastal Plain flora. Yet Walter's brief Latin descriptions have at times remained puzzling to later writers, with his names not given their proper status and employed for the appropriate species or relegated to synonymy.

A series of writers has addressed the names in Walter's book, many examining a single species of interest, others dealing with a genus or family. Hitchcock (1905) has surveyed the grasses, Dayton (1952) the pines, Wilbur (2002) the oaks, and Ward (2010a) the plants Walter named *Melanthium* (Liliaceae), and (2010b) those he named *Hedysarum* (Leguminosae). The present task is to investigate and establish the correct names of those plants Walter recognized as orchids (Orchidaceae).

The circumstances of Walter's work have been described to some extent elsewhere (Ward 2007d, 2008, 2009, and cited references). Walter kept no herbarium (Ward 2007a), and his 1056 descriptions were always short and sometimes cryptic. His contact in 1787 with the Scottish plant explorer John Fraser, though brief, was of importance in the preparation of the *Flora*, for Fraser claimed, by his travels in the Carolinas and Georgia, to have extended Walter's plant knowledge beyond the coastal plain. A number of Fraser's specimens within the Fraser/Walter folio herbarium, Natural History Museum, London (BM), have been considered neotypes or lectotypes of Walter's names (Ward 2007b, 2007c). The extent of Fraser's contribution to the content of Walter's book is uncertain, for Fraser's own statements are questionable (Ward 2007a). The possibility will be considered here that Walter obtained and perhaps grew plants from the Carolina mountains independently of Fraser. This conjecture is based on the large proportion of the orchids described by Walter that must have come from outside his stated collection range, and the unusual detail of their description

which implies access to fresh materials. And concern will be expressed that a number of Walter's new names yet to be confidently identified, if they were to be matched with species of the coastal plain and neotypified, would be prior to and thus replace long-familiar names of our floras.

Fifty-five species of orchid occur within the Carolinas (Radford et al. 1968). Of these, 24 are found on the coastal plain, the area in which Walter is known to have traveled and collected. Of this reduced list, only 6 are of distinctive species, readily separated from congeners, and are of sufficient frequency to be likely Walter observations, while 5 others are of groups of closely related species. Thus one might anticipate that the *Flora*, insofar as it was representative of coastal plain plants, should contain no more than 11 species of orchids.

Walter named and described 16 species of orchid. He placed these species in five genera—*Arethusa*, *Cypripedium*, *Limodorum*, *Ophrys*, and *Orchis*—taken from Linnaeus (1762). By present assessment, these sixteen species are assigned to at least eight modern genera—*Calopogon*, *Cleistes*, *Cypripedium*, *Hexalectris*, *Platanthera*, *Pogonia*, *Ponthieva*, and *Spiranthes*. Then, depending on interpretation of Walter's descriptions, possibly to four more—*Habenaria*, *Isotria*, *Liparis*, or *Triphora*.

Other orchid species of the Carolina coastal plain appear not to be associated with names used by Walter: *Epidendrum conopseum* (very rare, but known in Berkeley County), *Pteroglossaspis ecristata* (very rare, but known in Berkeley County), *Habenaria lacera* (very rare), *H. repens* (frequent; aquatic), *Malaxis spicata* and *M. uniflora* (rare, but known in Berkeley County), *Platanthera blephariglottis* (frequent), *P. clavellata* (frequent), *P. flava* (infrequent), *P. nivea* (infrequent), *Tipularia discolor* (common).

For one who is familiar with Walter's *Flora*, his treatment of the orchids will be seen as strikingly detailed. In most other genera of his book, Walter's practice was to describe the plant with few words, at times no more than two or three, but usually with a short phrase equivalent to, and sometimes identical to, those of his admired model, Linnaeus. But in species of the Orchidaceae his style was appreciably more thorough. His orchids were described, on average, with 15.3 words. No species received less than nine words; one, *Arethusa spicata*, was given a description of 37 words. No other species in his *Flora* received that level of attention.

Why Walter's orchids were given such exceptional attention may be of importance. Walter stated in his introduction that he had grown the plants of his book. His statement was unequivocal (in transl.): "for a long time he [Walter] has cultivated in his own garden the very many plants which he describes." Even so, there are exceptions, for example the Fraser Fir, *Abies fraseri* (his *Pinus cedrus*), where Walter described only the cone and was clearly unaware of the un-pine-like foliage of this montane tree (Ward 1962). This is one of an appreciable number of species from outside his stated collection area that may have been brought to him by Fraser (Ward 2007b).

Walter's orchids not only illustrate his access to non-local species, but perhaps bring a greater degree of understanding of their source. Fraser (1789) stated that before his arrival in the Carolinas in the fall of 1786, Walter had described 640 species; by his departure in the early spring of 1788 he had increased Walter's tally to 1060. Fraser thus claimed credit for 420 of the species described by Walter. Among this number he further reported there were "upwards of 200 new species."

Yet analysis of the ranges of species described by Walter leaves only a modest number, no more than 103 (or 10%), that are known only outside the area from which Walter stated he had acquired his specimens (Ward 2007a). [Among these few are the 20 Fraser specimens designated as lectotypes (Ward 2007b, 2007c).] For over 90% of the species of the *Flora*, Walter would have had no need to rely on the incomplete, often-fragmentary materials gathered by Fraser.

Walter's orchids present a strikingly different story. As noted (above), 55 species of orchid are to be found in the Carolinas, with only 24 known to occur within Walter's area. Thus more than half, or 31 (56%), of these species are known only outside the collection area described by Walter. Walter's collection success closely parallels this distribution frequency. Of the 16 orchids known to Walter, perhaps 10 (63%) were unlikely to have been found by Walter within his stated collection range. These ratios contrast strongly with the one-tenth ratio found in the *Flora* as a whole. So why did Walter appear to know South Carolina's orchids so much more thoroughly than the state's flora as a whole?

A possible explanation is offered here for this disparity between the percentage of orchids known only outside Walter's collection area, and the percentage of similarly-located species in the full *Flora*. The detailed descriptions given by Walter to the orchids would seem to require that they were indeed grown by him, or observed in the field, rather than be materials brought to him by Fraser. If Fraser had been the source, and the plants had been obtained during his only collecting opportunity of the 1787 season, Walter could not have grown the plants to flowering in time to insert the descriptions before Fraser left the Carolinas in early 1788, carrying Walter's manuscript to London for publication.

It is apparent that Walter took great interest in the orchids, sufficient to provide him with the observations necessary for his extended descriptions. It is possible that he did not grow *all* of his species in his garden, and that, in spite of his statement to the contrary, he or other parties than Fraser had ventured into the Carolina mountains in the years prior to Fraser's journey. This interpretation seems not to have been expressed before. It greatly eases the difficulty of understanding how Fraser was able to acquire *all* the many species presumed to be his contribution to the *Flora*.

Walter's treatment of the Carolina orchids illustrates another little-appreciated consequence. This is the risk to current nomenclatural stability that lies in the existence of plant names, validly published and of very early date, but not matched with modern names. Although from time to time authors have identified one of Walter's descriptions and have put forward a wholly unfamiliar name or new combination, there still remain a significant number of such unidentified names, awaiting only the attention of a young turk to be brought forward. [A recent example: Goldman 1998.] The act of neotypification of the Walter name removes doubt of his plant's identity and obligates modern authors to accept the new name. Within the 16 described orchids, no less than 4 names (25%) appear to hold such potential—*Orchis lata* Walt., *Orchis calcarata* Walt., *Limodorum autumnale* Walt., and *Arethusa foliosa* Walt. Though here held back by the present authors' expressions of doubt, another author may not be so restrained. Attention needs be given to the very appreciable number of potentially disruptive names found throughout Walter's *Flora*.

The 16 species Walter recognized in the genera *Arethusa*, *Cypripedium*, *Limodorum*, *Ophrys*, and *Orchis* are listed below in the order given when originally published, with their modern identifications. Walter's descriptions (in Latin) are given in full, in italic. Words which he italicized and thus emphasized are shown in roman. Abundance within South Carolina is largely inferred from the county-record maps prepared by Radford et al. (1968). A measure of the likelihood of correct identification is attempted by uniform usage of modifying adverbs preceding the name, where a simple assertion means "little room for doubt," and "probably" and "possibly" indicate increasing levels of uncertainty.

LIST OF SPECIES

Walter's name: *Orchis ciliaris* (p. 220). Linnaeus, Sp. Pl. 939. 1753.
Walter's description: bulbis indivisis, nectarii labio-lanceolato ciliato, cornu longo. Varietates, floribus luteis, et flor. albis.
Modern name: **Platanthera ciliaris** (L.) Lindl. [= *Habenaria ciliaris* (L.) R. Br.], **Platanthera cristata** (Michx.) Lindl. [= *Habenaria cristata* (Michx.) R. Br.], or **Platanthera blephariglottis** (Willd.) Lindl. [= *Habenaria blephariglottis* (Willd.) Hook.]
Comments: *Platanthera ciliaris*, *P. cristata*, and *P. blephariglottis* are frequent in eastern SC. The first two have orange to orange-yellow flowers; Walter's "*cornu longo*" better fits the first. He noted both dark yellow and white-flowered varieties; he may also have included the white-flowered *P. blephariglottis*, or he may have encountered hybrids among these species. Spm. 78-A of the Fraser/Walter herbarium was labeled "*Orchis*," apparently by Fraser. It may well be *Platanthera (Habenaria) ciliaris*, as annotated by O. Ames. No neotype has been selected.

Walter's name: *Orchis lata* Walter (p. 220)
Walter's description: *alba, bulbis indivisis, nectarii labio integro lato revoluto, cornu sublongo tenui*.
Modern name: Possibly **Platanthera nivea** (Nutt.) Luer [= *Habenaria nivea* (Nutt.) Spreng.]

Comments: If this species, infrequent in eastern SC. White flowers suggest *Platanthera nivea*. No specimen has been identified in the Fraser/Walter herbarium. Though *Orchis nivea* Nuttall (1818) is later and would be displaced, the identification of Walter's plant is uncertain. No neotype has been selected.

Walter's name: *Orchis ophioglossoides* (Linnaeus) Walter (p. 220). *Arethusa ophioglossoides* Linnaeus, Sp. Pl. 951. 1753.
Walter's description: *alba, bulbis indivisis, folio unico scapum vaginante, floribus minimis paniculatis, cornu brevi, nectarii labio lanceolato integro.*
Modern name: **Pogonia ophioglossoides** (L.) Ker
Comments: Frequent in coastal SC. Spms. 77-C and 77-D of the Fraser/Walter herbarium are this; both were labeled "*Ophrys*" by Fraser. The binomial employed by Walter was a new combination, one of the very few occasions where he chose to assign the species to a genus different from that employed by Linnaeus.

Walter's name: *Orchis habenaria ?* (p. 220). Linnaeus, Syst. Nat. ed. 10. 2:1242. 1759; misapplied.
Walter's description: *alba, bulbis indivisis, nectarii labio longo-tripartito, laciniis setaceis, pedunculis multifloris, foliis lanceolatis (cornu mediocri).*
Modern name: **Habenaria quinqueseta** (Michx.) Eaton
Comments: Rare in SC (but known in Berkeley Co.). Walter's description well corresponds to this plant; the white flowers and three-parted lip ("*labio longo-tripartito, laciniis setaceis*") seem exact. No specimen is in the Fraser/Walter herbarium. Not *Orchis habenaria* L., of the West Indies.

Walter's name: *Orchis calcarata* Walter (p. 220)
Walter's description: *albo-viridis, bulbis indivisis, nectarii labio septemcalcarato, cornu longissimo.*
Modern name: Probably **Platanthera lacera** (Michx.) G. Don [= *Habenaria lacera* (Michx.) Lodd.]
Comments: If this species, rare and inland in SC, frequent in western NC; possibly a Fraser discovery. The description, though brief, seems unambiguous: Walter's "*albo-viridis*" flowers are appropriate; his "*labio septemcalcarato*" suggests the fringed lip; the spur is long, "*cornu longissimo.*" Spm. 78-D of the Fraser/Walter herbarium is *P. lacera*; it was labeled "*Orchis*" by Walter. Walter's name is not cited in modern treatments, even in synonymy. But the epithet is prior to *Orchis lacera* Michaux (1803) and would require use if the description were determined to be of the modern *P. lacera* and a specimen of that species were selected as Walter's neotype.

Walter's name: *Ophrys trifolia* Walter (p. 221)
Walter's description: *bulbis fasciculatis, foliis radicalibus ovatis submagnis planis, scapo trifolio, floribus albo-viridibus adscendentibus, nectarii labio integro lato subtriangulari.*
Modern name: Possibly **Liparis liliifolia** (L.) Richard
Comments: If this species, unknown in eastern SC, though frequent in NC and western SC; possibly a Fraser discovery. The lengthy description should permit confident identification. The flowers of *Liparis liliifolia* do indeed have broad entire subtriangular lips ("*labio integro lato subtriangulari*"), and the leaves are basal and ovate ("*radicalibus ovatis*"). But the scape is not "*trifolio*," and the lips are pale purple, not pale green. A more apt identification would be welcome. The name *Ophrys trifolia* is not in use. No specimen has been identified in the Fraser/Walter herbarium. No type has been selected. In manuscript review, *Pteroglossaspis ecristata* (Fern.) Rolfe [= *Eulophia ecristata* (Fern.) Ames] was suggested. If that species, very rare in SC, but known in Berkeley Co. If so determined, Walter's epithet would displace that of Fernald (*Cyrtopodium ecristatum*, 1897).

Walter's name: *Ophrys fimbriata* Walter (p. 221)
Walter's description: *radice fibrosa cruciformi, caule folioso, floribus rubris paucis, nectarii labio indiviso fimbriato.*
Modern name: Probably **Platanthera psycodes** (L.) Lindl. [= *Habenaria psycodes* (L.) Spreng.]
Comments: If this species, unknown in SC, in NC only in western mountains. Walter's "*floribus rubris paucis*"

well corresponds to the small rose-purple flowers of *P. psycodes*. The western range of that species suggests it may have been a Fraser discovery. Flower color might also suggest *Platanthera cristata* or *P. ciliaris*, as does the "*fimbriato*" lip; but these species better fit Walter's *Orchis ciliaris* (as treated below). The name *Ophrys fimbriata* has not been used in American floras. No specimen has been identified in the Fraser/Walter herbarium. No neotype has been selected, nor is one needed in light of the earlier basionym, *Orchis psycodes* Linnaeus (1753).

Walter's name: *Ophrys barbata* Walter (p. 221)
Walter's description: *bulbo rotundo, petalis ovatis, nectarii labio indiviso, apice dilatato truncato supra ad medium barba colorata.*
Modern name: Probably **Calopogon tuberosus** (L.) BSP., possibly including **Calopogon barbatus** (Walt.) Ames and **Calopogon pallidus** Chapm.
Comments: *Calopogon tuberosus* is frequent in eastern SC. Walter would surely have known it, also perhaps the much rarer *C. barbatus* and *C. pallidus*. Walter's description does not permit judgment as to which of these species he meant by his *Ophrys barbata*—the lip is bearded in all. Spm. 77-E of the Fraser/Walter herbarium is clearly a *Calopogon*. Its original label bears only the single word "*Ophrys*" in Fraser's hand; it was later annotated as "*Ophrys barbata / Calopogon parviflorus*" by A. A. Eaton. Goldman (1998) stated the specimen to be "Walter's type" of *C. barbatus*, but he then identified it as *C. multiflorus* Lindl. [*Calopogon multiflorus*, however, is nearly absent from the Carolinas and Georgia (one station in NC, with unverified reports from SC and GA).] Goldman then selected a specimen from Baker County, Florida, as neotype for *Ophrys barbata* Walt., and proposed conservation of Walter's name with this new type. His proposal was promptly accepted. This action retains the historic interpretation of *Calopogon barbatus*.

Walter's name: *Limodorum praecox* Walter (p. 221)
Walter's description: *radicibus fibrosis, foliis ensiformibus, spica serie fimplici florum spirali, floribus albis, nectario sessili, filamento brevi.*
Modern name: **Spiranthes praecox** (Walt.) Watson
Comments: Infrequent on SC coastal plain. Spm. 65-D of the Fraser/Walter herbarium appears to be this. It was labeled "*Limodorum*" by Fraser, and has been annotated as "*praecox*" (by O. Ames?). There is no indication it was seen or used by Walter. But the specimen is of good quality and has been selected (Ward 2007c) as neotype for *Limodorum praecox* Walt., basionym of *Spiranthes praecox* (Walt.) Watson.

Walter's name: *Limodorum autumnale* Walter (p. 221)
Walter's description: *floribus majoribus, caule bracteisque pubescentibus, caule foliis obsito,* spica serie dublici spirali.
Modern name: Probably **Spiranthes odorata** (Nutt.) Lindl., possibly **Spiranthes cernua** (L.) Rich.
Comments: Both *Spiranthes odorata* and *S. cernua* are infrequent to rare on the SC coastal plain, the second becoming common westward. Walter's use of "*autumnale*" is appropriate for these fall-flowering species. The relatively large flowers of *S. odorata* and Walter's use of "*floribus majoribus*" incline one toward *S. odorata*. Spm. 65-E of the Fraser/Walter herbarium was labeled "*Limodorum*" by Walter and has been annotated "*Spiranthes cernua*" by O. Ames. No neotype has been selected.

Walter's name: *Cypripedium Calceolus* (p. 222). Linnaeus, Sp. Pl. 951. 1753.
Walter's description: *radicibus fibrosis, foliis ovato-lanceolatis caulinis, caule multifloro, flore luteo.*
Modern name: **Cypripedium parviflorum** Salisb. var. **pubescens** (Willd.) O. W. Knight [= *Cypripedium calceolus* L. var. *pubescens* (Willd.) Correll]
Comments: Restricted to mountains of western NC, thus surely a Fraser discovery. Spm. 39-A of the Fraser/Walter herbarium is this, and bears Fraser's hand ("*Cypripedium Calceolus*").

Walter's name: *Cypripedium reginae* Walter (p. 222)
Walter's description: *radicibus fibrosis, foliis ovato-lanceolatis caulinis, caule multifloro, flore albo magno.*

Modern name: **Cypripedium reginae** Walt.
Comments: Very rare: in the Carolinas, known only in NC (2 counties). Spm. 39-B of the Fraser/Walter herbarium is labeled "*Cypripedium Reginae*" in Fraser's hand. It has been marked as "type" (by O. Ames?), but the designation was not published. Since Walter could most likely have seen this species only through the agency of Fraser, this specimen (or another of the same gathering) may well have used by him. Thus spm. 39-B has been designated (Ward 2007c) lectotype of *Cypripedium reginae* Walt.

Walter's name: *Arethusa divaricata* (p. 222). Linnaeus, Sp. Pl. 951. 1753.
Walter's description: *radice fibrosa, foliis lato-subulatis, capsula oblonga subtereti sexsulcata, petalis tribus lanceolatis purpureis suberectis, aliis duobus latis incarnatis, caule unifloro.*
Modern name: **Cleistes divaricata** (L.) Ames
Comments: Frequent on SC coastal plain. Spm. 8-E of the Fraser/Walter herbarium (BM) was labeled "*Arethusa Divaricata*" by Fraser. Walter very probably correctly identified Linnaeus' *Arethusa divaricata*.

Walter's name: *Arethusa racemosa* Walter (p. 222)
Walter's description: *radice tuberosa bipartita, foliis radicalibus ovatis nervosis, scapo longo subnudo racemifloro, floribus parvis alternis pedicellatis, petalis patulis aequalibus albidis, capsulis* ovatis.
Modern name: **Ponthieva racemosa** (Walt.) Mohr
Comments: Occasional in coastal SC. The label of spm. 8-D ("*Arethusa racemosa*") is in Walter's hand. But since the species would have been available to Walter near his home and the label bears a 3-digit number ("??9") which indicates the specimen to be a Fraser collection, it may not have been seen by Walter until after completion of his manuscript. Blake (1915) correctly called it "an excellent specimen." It has been selected (Ward 2007c) as neotype for *Arethusa racemosa* Walt., basionym of *Ponthieva racemosa* (Walt.) Mohr.

Walter's name: *Arethusa spicata* Walter (p. 222)
Walter's description: *radice tuberosa, caule sesquipedali succulento aphyllo, floribus bracteatis sessilibus alternis spicatim positis, petalis aequalibus ovatis conniventibus flavescentibus striis purpureis, nectario longitudine petalorum rugosa subtrilobo, lobis lateralibus brevioribus erectis, colore petalorum, lobo medio purpureo propendente, capsula columnari angulare*.
Modern name: **Hexalectris spicata** (Walt.) Barnh.
Comments: Infrequent throughout. As Blake (1915) has stated, Walter's diagnosis is "quite distinctive" of this species. There is no specimen in the Fraser/Walter herbarium. A specimen from Richland County, South Carolina, has been selected (Ward 2008) as neotype for *Arethusa spicata* Walt., basionym of *Hexalectris spicata* (Walt.) Barnh.

Walter's name: *Arethusa foliosa* Walter (p. 223)
Walter's description: *radice bulbosa, caule folioso unifloro, foliis alternis brevibus nervosis, flore terminali lineari albido, capsula oblonga hexangula*.
Modern name: Probably **Triphora trianthophora** (Sw.) Rydb.; possibly **Isotria verticillata** (Muhl. ex Willd.) Raf.
Comments: The name *Arethusa foliosa* is not recorded in modern floras, even in synonymy. Walter's rather detailed description cannot be wholly matched with any orchid of eastern America. But Walter must have had *something*, and if his plant were to be identified, his epithet could be prior to a familiar name. Two species come to mind, each rare in the Carolinas. *Triphora trianthophora* is almost restricted to the mountains, yet has been found in Berkeley Co.; *Isotria verticillata* is wholly unknown on the coastal plain (possibly reaching Walter via the agency of Fraser). The flowers of *Triphora* are white ("*albido*"), its leaves cauline ("*caule folioso*") and short ("*brevibus*"); yet its flowers are only rarely single ("*unifloro*") and never terminal ("*terminali*"). *Isotria* bears solitary terminal flowers, and its elongate, narrowly lanceolate sepals conform to Walter's "*lineari*"; yet its perianth is purplish to green, and its distinctive whorled leaves could scarcely have been overlooked. No specimen has been identified in the Fraser/Walter herbarium. Walter's description is surely an amalgam

of features once seen and imperfectly remembered. No neotype has been selected. If *Arethusa foliosa* were determined to be the modern *Triphora trianthophora*, Walter's epithet would displace the basionym, *Arethusa trianthophora* Swartz (1800).

ACKNOWLEDGMENTS

We are grateful to Christine M. Housel for her preparation of the Spanish abstract. Alexander Krings and an anonymous reviewer suggested many helpful improvements!

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BOOK REVIEW

Tim Robinson. 2008. **William Roxburgh: The Founding Father of Indian Botany.** (ISBN-13: 978-186077-434-8, ISBN 10: 978-1-86077-434-2, hbk.). Joint publication of the Royal Botanic Garden Edinburgh and Phillimore & Co. Ltd., Phillimore & Co. Ltd., Healey House, Dene Road, Andover, Hampshire, England, SP10 2AA, U.K.). (**Orders:** The History Press, Sales (Phillimore & Co. Ltd), The Mill, Brimscombe Port, Stroud, Gloucestershire, England, GL5 2QG, U.K.; http://www.thehistorypress.co.uk/; 01453 883300 (International +44 1453 883300; 01453 883233 fax). £50.00, 286 pp., 150 b/w, 16 color, 8 ½" × 11".

This book is all but perfect. I just loved it! Mr. Robinson has created an all encompassing biography of one of botany's greats. There is something for everyone in this book. William Roxburgh was a medical doctor by training, having trained at the University of Edinburgh during the period of the Edinburgh Enlightenment. He spent the years 1776–1814 in India where he collected and catalogued the plants of India. As you can well imagine, the weather in Calcutta in the 1800 was less than perfect for preserving plants. Roxburgh trained and employed Indian artists to paint pictures of the plants. These pictures are exquisite and Mr. Robinson has been generous in putting so many of them in this book.

If you are interested in just Dr. Roxburgh's personal biography, Robinson manages to convey his personality and life through letters written by, to and about Roxburgh. Robinson even includes the family trees of Roxburgh's three wives and the fate of their children, and even includes the child of a union with an Indian woman.

Robinson has included all of Roxburgh's interests. Drawings of the plans for the Calcutta Botanical Garden are included in the book. Meteorology, development of plants to be used for dyeing fabrics, crops of peppers and spices, and sugar production were of interest to Roxburgh. Early in his stay in India, he researched several crops to produce hemp. England was at war with France, thus were unable to procure hemp from the Russians. Roxburgh tried several species to solve this problem. By the time he found an acceptable substitute, the war was over.

Robinson creates the political climate in India, England, and Scotland between various scientists competing for money, prestige, and power. It is fascinating. Because Robinson uses actual correspondence from the various parties, the reader gets drawn in to the story. Personal relationships, work habits, reliability of various employees, the problems of shipping plants and animals around the Cape of Good Hope are all part of the story. It is very entertaining.

If you are interested in the business end of the East India Company, Roxburgh's employer, there is a comprehensive tally of products, plants, and animals that he developed, shipped, investigated, and introduced into various milieus. He shipped thousands of plants to Kew Garden. He also planted or had others plant thousands of trees and plants he hoped would alleviate the "famine years" in India. He drew up plans for channeling the rain that fell during the monsoon season to ponds so the water would be available throughout the year.

I could go on forever about how wonderful this book. Apparently Mr. Robinson has spent many years cataloging the work of William Roxburgh. His admiration for the Father of Indian Botany is evident, and he has created an exquisite and fascinating picture of Dr. Roxburgh in this book. —*Kay Yount, Tarrant County Master Gardener and BRIT volunteer, Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A.*

BIOLOGICAL STATUS OF *CROTON BIGBENDENSIS* (EUPHORBIACEAE): SPECIES, VARIETY, OR INFORMAL VARIANT?

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ABSTRACT

The present article is a rebuttal to the paper presented by Henrickson (2010), in which he contends that Turner (2004) did not properly typify the species concerned, nor did he adequately justify its biological status. Evidence and discussion are presented here that it indeed is typified properly and that its biological status justifies recognition at specific rank.

RESUMEN

El presente artículo es una refutación al presentado por Henrickson (2010), en el que sostiene que Turner (2004) no tipificó adecuadamente la especie implicada, ni justifico apropiadamente su status biológico. Se presentan aquí la pruebas y discusión de que está tipificada adecuadamente y que su status biológico justifica su reconocimiento en el rango específico.

Henrickson (2010), in the "revisitation" of the recognition and formal description of *Croton bigbendensis* (Turner 2004), finds fault with both the process of typification and the biological reality of the taxon. Regarding the typification, he noted (pp. 295–296):

"Unfortunately, in his paper he cites two herbarium specimens as holotypes, one pistillate (*Turner 22-204A*) and one staminate (*Turner 22-204B*), each given a separate number. Though collected at the same time from the same population (a single gathering), the International Code of Botanical Nomenclature (McNeill et al. 2006) does not allow two separate specimens with two numbers to be designated as separate holotypes [ICBN Art. 9.1- "A holotype of a name or a species or infraspecific taxon is the **one** specimen or illustration used by the author, or designated by the author as the nomenclatural type (emphasis mine)] and thus the name was not validly published and is considered an invalid name (Kanchi Gandhi, pers. comm.; see International Plant Name Index). **A holotype can consist of more than one sheet of a single specimen (ICBN Art. 8.3) if clearly noted and can consist of more than one plant in a single gathering (Art 8. 2)** [emphasis mine], but the designation of two separately numbered specimens, mounted on separate sheets, each named as holotype (Turner 2004, pp 81 & 82.), renders the specimens syntypes (Art. 9.4, ex 1.) and therefore no holotype exists and the name is not validly published."

It should be noted (in reference to my bolded print in the quote above from Henrickson) that I designated two sheets as **the** holotype, **each bearing the same collection number:** the pistillate plant designated as 22-204a, the staminate as 22-204B. It should also be noted (hence the bold type) that the two sheets have the same number, were collected at the same site on the same day at the same time, and photographs of both pictured and the two sheets representing the single type sit on top of each other in the University of Texas herbarium (TEX-LL). Unlike the observation posited above by Henrickson, the two holotype sheets do bear the same collection number and are **clearly noted** as the holotype, one of these lettered A, and one B, for the reasons given above. Since the sheets concerned are not syntypes, Art. 9.1 does not apply. I conclude, therefore, that the name is properly typified and validly published.

How can one be more explicit as to designation? But if one wishes to get hyper technical, as Henrickson's bent might be, one need only read Art 8.3 a little further where it states that "A specimen may be mounted as more than one preparation, as long as the parts are clearly labeled as being part of that same specimen. What could be clearer than my designation: everything clearly labeled and bearing the same collection number! Example 2, given under Art 8.3 confirms the legitimacy of my designation—the holotype specimen of *Delissea eleeleensis* H. St. John, is mounted as two preparations, a herbarium sheet and a bottled preparation of an inflorescence bearing the same collection number of the herbarium sheet, much as in my designations.

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Example 4 notes that "The holotype of *Cephaëlis acanthacea* Steyerm., *Cuatrecasas 16752* (F), consists of a single specimen mounted on two herbaruim sheets, labeled 'sheet 1' and 'sheet 2.' Although the two sheets have separate herbarium numbers, F-1153741 and F-1153742, respectively, the cross-labeling indicates that they constitute a single specimen."

The dioecious *Croton bigbendensis* is only fully represented as a species by at least two plants, which show the staminate and the pistillate condition. A single plant would be acceptable as the nomenclatural type, but the two plants more fully define the species. The original typification clearly and explicitly represents the two plants as part of a single specimen.

Biological Status of *Croton bigbendensis*

Regarding the procedures of his revisitation, Henrickson informs the reader that "Data were collected from all specimens at TEX-LL (n=296) with 41 from trans-Pecos Texas identified by Turner as "*Croton bigbendensis*" plus six of my specimens that are clearly referable to that taxon, 72 from typical *Croton dioicus* in trans-Pecos Texas (west of the River), 98 from *C. dioicus* from cis-Pecos Texas (east of the Pecos River) and adjacent New Mexico, and 85 from *C. dioicus* from Mexico." All of these plants were reexamined by me in the present study, except for the six specimens of *C. bigbendensis* collected by Henrickson, these presumably not as yet mounted; at least they were not found among the current collections at TEX-LL.

In the current reassessment of *Croton bigbendensis* and *C. dioicus*, I have studied again the two taxa concerned, most all of which had been annotated by me during my initial studies. Not a single sheet, however, was formally annotated by Henrickson, even before or after his publication. His failure to annotate specimens of *C. dioicus* was of no concern, for the taxon is relatively invariant throughout its range, but his failure to annotate sheets of *C. bigbendensis,* or the hypothetical intergrades has made it difficult for me to understand his assessment. It should also be noted that Henrickson did not borrow, or annotate, the large number of collections of this complex housed at SRSC, the herbarium out of which I was working at the time of my interest in the taxa concerned.

My restudy of the *Croton bigbendensis-C. dioicus* complex has not changed my original conclusions. There are clearly two taxa in the trans-Pecos (Fig. 1), one of these a robust erect, much-branched, perennial herb to 1 m high, having mostly linear lanceolate upper leaves (*C. bigbendensis*), the other a low, mostly compact perennial herb with more nearly ovate leaves, the blades usually obtuse or rounded at the apices (*C. dioicus*). The two taxa are readily recognized in the field, where they often exist as large populations. In my original publication of *C. bigbendensis*, I was unaware of the extension of *C. dioicus* into southern Brewster County, where they approach populations of *C. bigbendensis*, mainly because at the time of my original publication I had not reexamined the TEX-LL collections, because of my Alpine residence during that period. But, during my many field trips in that region at the time, I never found the two taxa growing together or near each other.

Subsequently, however, I discovered a collection at TEX-LL (*Warnock s.n.* Persimmon Gap. Chisos Mountain area, 2 May 1937) that documented their co-occurrence in southern Brewster Co., if the sheet concerned is not an error in mounting. Henrickson himself, by penciled notation ("= Bigbendensis"), recognized the two specimens on that sheet as distinct "somethings" (having failed to annotate *C. dioicus*, which bore my annotation with this name). The only other area or population in which the two taxa have been noted as growing together has been in collections made by me, called to the fore by Henrickson (p. 299):

> "Two collections made by Turner in 2004 in gypsum soils in northeastern Culberson County, Texas (Fig. 2) illustrate the problem with Turner's interpretation of the taxon. *Turner 24-409* (TEX) is a pistillate plant considered to be *C. dioicus* that has oblong-ovate leaves with rounded tips, 26.5 x 8.2 mm (l/w ratio 3.2) and internodes to 42 mm long. It is growing with/near a staminate specimen (*Turner 24-402*) (TEX) that has lanceolate, acute-tipped leaves, 31 x 6.5 mm (l/w ratio 4.7) with internodes to 46 mm long that is identified as "bigbendensis." The two specimens appear identical [to Henrickson] in stature, coloration etc. and both are in flower. But while the specimen he [Turner] considers to be "bigbendensis" is well out of its normal range (Fig. 2), the specimen of *C. dioicus* bears a hand-written note by Turner "growing with *C. bigbendensis* (24-402); no intermediates seen." I see this as just variation within a population of *C. dioicus*."

Henrickson, in his evaluation of the taxa concerned, attempting to make his study more quantitative than my own, constructed a graph (his Fig. 1) on which was positioned those plants referable (in his opinion)

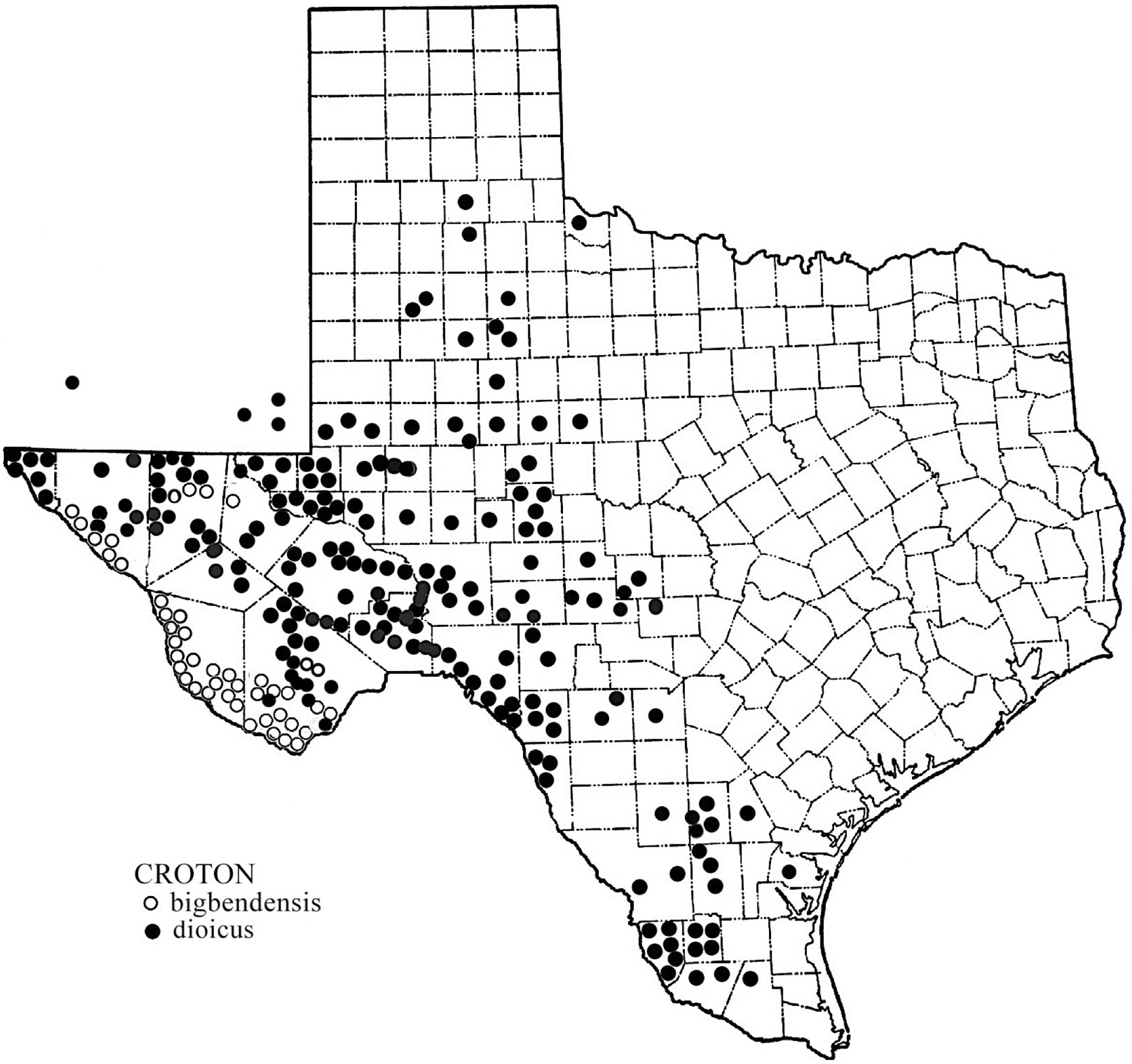

Fig. 1. Distribution of *Croton bigbendensis* and *B. dioicus* in Texas and New Mexico.

to *C. bigbendensis*, and those referable to *C. dioicus*. The data used to construct the graph were said to be internode length (the longest internode observed on the plants concerned) and leaf blade length/width ratios. To his credit, most of the measurements were penciled on most of the sheets that he examined. The measurements, however, were made from herbarium sheets from over a very large area, which merely showed eclectic variation of the taxa concerned. What would have been more meaningful were graphs for individuals from populations in the field, especially where the two taxa might occur together, suggesting gene exchange—in short, following the procedures of Edgar Anderson (1949, 1954), using scatter diagrams, with care given to the particular measurements recorded (1954). Thus, Anderson (1954) would have demanded that leaf measurements be made consistently from leaves at a given node, and internodal length, likewise, say between the 6th and 7th nodes, if such could be determined.

Regardless, I was unable to relate Henrickson's scatter diagrams to the problems at hand, not only because they were not populational in nature, but also because the sheets were not formally annotated by him.

This brings me to Henrickson's Figure 2, "Distribution of *Croton dioicus* and "bigbendensis" in trans-Pecos Texas, based on specimens so identified by Turner at TEX-LL)." Henrickson mapped 10 plants and/

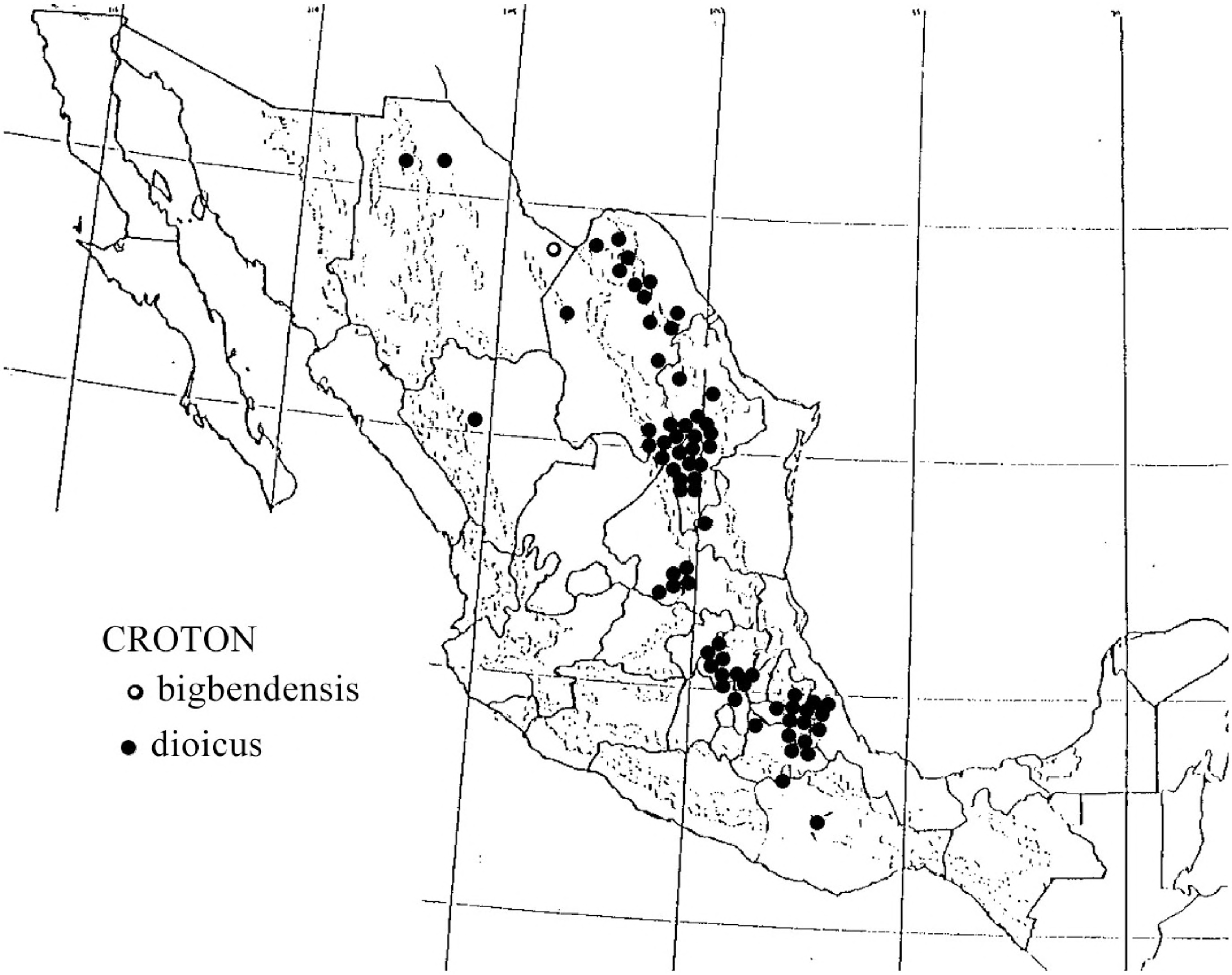

Fig. 2. Distribution of *Croton bigbendensis* and *C. dioicus* in Mexico.

or populations of "bigbendensis" as occurring in southern Brewster Co., 10 such collections from adjacent Presidio Co. and 2 from Hudspeth Co., most of these occurring along the Rio Grande. He notes these to be so identified by myself. My assumption is that he would not have identified the collections concerned as *C. bigbendensis*, but rather would have dubbed them *C. dioicus*. As already noted, he failed to formally annotate any of the sheets concerned, either at TEX or SRSC. On this same map, Henrickson included a series of open squares that were said to be "intergrades," 7 of these in Brewster Co, 1 in Presidio Co. and several others in more western counties. Unfortunately, he did not list the so-called intergrades in his paper, nor did he annotate any of the sheets on file at TEX-LL, as such, but I could infer some of these by location and penciled comments on some of the mapped sheets. Thus, on the single so-called intergrade from Presidio Co. (*Butterwick & Strong 829*), Henrickson had scribbled in pencil "Closer to" with an arrow pointing to *Croton dioicus* (my formal annotation prior to my discovery of *C. bigbendensis*). I could locate only one other possible, so-called intergrade among the Brewster Co, sheets of *C. bigbendensis* on file at TEX-LL, this being *Baker 1512*, in which Henrickson placed, in pencil, the word "No!" next to my inked annotation, "C. bigbendensis B.L. Turner." In my opinion, both of these so-called intergrades are typical elements of *C. bigbendensis*. Among the *C. dioicus* specimens on file at TEX-LL (Nine Point Mesa, *Webster & Westford 32586*) I found one plant with the penciled "No!" placed next to an old annotation label of mine inked in as *B. bigbendensis*. My original annotation was in error; it should have been *C. dioicus*, but not an intergrade, as suggested by Henrickson's notation.

More egregious is Henrickson's contention that pressed specimens identifiable (to him) as "bigbendensis" were found well within the Mexican range of *C. dioicus* (e.g., states of Nuevo Leon, Hidalgo and Puebla). I

have examined all of the mounted sheets of from these states at TEX-LL (none annotated by Henrickson) and I would identify these as part of the fabric of *C. dioicus*, these annotated accordingly. Henrickson did call attention to a single collection from the Samalayuca dunes of north-central Chihuahua that I had not examined in my initial studies; he thought this might compare well with "bigbendensis." I take the sheet concerned to be closer to *C. dioicus*, but perhaps an undescribed taxon, having larger stellate hairs that seem atypical of *C. bigbendensis*, and larger ovaries and peculiar leaves. While Henrickson called attention to the plant concerned, he did not annotate or place notes upon the specimen. I annotated the sheet as perhaps undescribed, but mapped this as *C. dioicus* in Figure 2.

Biological Status and Taxonomic Rank of *Croton bigbendensis*

The above observations and comments seem disproportionate to the problem at hand: whether *C. bigbendensis* be recognized as a sound biological taxon, or not. In my opinion, yes! Most any experienced field taxonomist could recognize the populational elements concerned at a glance, surely each deserving of a name. Should it be called a species or a variety? Lacking adequate populational data in regions of contact, it is difficult to say. If the populations coexist without clear intermediates, it seems best to threat these as species, as has been argued elsewhere (Turner and Nesom 2000); if it can be shown that the two taxa intergrade to some significant extent near regions of contact they are perhaps better treated as infraspecific taxa. Henrickson, however, has a different point of view; his concluding paragraph reads as follows (p. 300):

> "But while the data do show the existence of plants with narrower leaves and longer internodes in the southern margin of the trans-Pecos Texas, the plants are not clearly distinguished from *C. dioicus*. Due to the blending of the quantitative characteristics used to define "bigbendensis," using Turner's own criteria (Turner and Nesom 2000), the taxon would be considered a variety of *C. dioicus*. But, I see no reason to recognize "bigbendensis" at any rank, but to incorporate it's characters into the known variation of the wide ranging and poorly studied *Croton dioicus*. **As it stands, *Croton dioicus* is a very distinctive species, easily recognized over its range by substantial characters.** I see no value in recognize [sic] peripheral populations that differ in minor quantitative characters as equal species. Certainly in this instance there is no evidence that "bigbendensis" is a good biological species. But we must remember that even with field observations, without experimental data, such taxonomic decisions are just opinion."

Henrickson (2010) has not, in my opinion, as discussed above, presented adequate quantitative populational data to show that the taxa concerned intergrade near regions of contact. Indeed, to paraphrase his sentence bolded in the above paragraph, I can state this with certainty. **As it stands, *Croton bigbendensis* is a very distinctive species, easily recognized over its range by substantial characters.** Henrickson's final sentence is true, depending upon his definition of experimental data; certainly none is provided in his quantitative assessments of the taxa concerned here. Indeed, most all of the taxa among higher plants generally, are lacking in experimental data, but this does not preclude our recognition of a multitude of species, mostly by inference, from what one understands about experimental methods and quantitative analysis as applied to populations. No doubt, the final arbiter in all this ado will be the application of DNA data. I look forward to the systematic conclusions drawn from such studies.

ACKNOWLEDGMENTS

I am grateful to my long-time colleagues, Guy Nesom and Mike Powell, for reading the paper and making helpful suggestions. Distribution maps (Figs. 1, 2) are based upon specimens on file at SRSC and TEX-LL. One anonymous reviewer's comments are greatly appreciated.

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BOOK REVIEW

Kathryn Mauz. 2011. **An Agreeable Landscape: Historical Botany and Plant Biodiversity of a Sonoran Desert Bottomland, 1855–1920.** (ISBN 13: 978-1-889878-35-5; ISSN 0833-1475; pbk.). SBM #35. Botanical Research Institute of Texas, 1700 University Dr., Fort Worth, Texas 76107-3400, U.S.A. (**Orders:** http://www.brit.org/brit-press/books/sbm-35; orders@brit.org; 817-332-4441 × 33). $30.00, 234 pp., b/w and color figures, 6.5" × 9.5".

Every so often we are privileged to have a great work like the "Agreeable Landscape." This work vividly brings us to the vanquished wetlands of the Santa Cruz Valley obliterated by the now million-strong urban sprawl of greater Tucson, Arizona. The back cover of this information-packed book tells that "John Russell Bartlett found that it presented an agreeable landscape: irrigated fields, fine grass, and a winding line of tree canopies down the valley of the Santa Cruz River at Tucson, southern Arizona, in 1852." Dr. Mauz's precision documentation of the demise of a riverine empire nested in the upper reaches of the Sonoran Desert provides verifiable detail that mirrors the impact of exploding human population in arid lands around the world. We have all heard how fragile wetlands are, especially in deserts, but this volume, largely anchored by botanical specimens, explores new dimensions.

This work is primary research built on a wealth of historic information, specimens, on-the-ground fieldwork, modern geography and more—a vast knowledge uncovered and succinctly interpreted. The author personally tracked down an almost "hidden" wealth of specimens in distant herbaria and carefully studied and interpreted each and every one, tying them to the "bigger picture." Read through or just turn to any part of this book and you will be impressed by the underlying scholarship and joy of discovery. You will meet the botanical collectors and others who provided the foundation material that will connect you to a paradise lost. You will meet men, and some women whose voices got through, who were witnesses to the demise of wetland lifelines. Funding agencies and institution administrators should take notice of the priceless value of life's heritage preserved in herbaria.

The species accounts (annotated flora catalog) provide encapsulated interpretations of the flora. And again, I have to tell you that the power of this volume is the attention to detail, scientific accuracy, and original interpretations. Just in case some botanists care to quibble about identifications, the specimens are carefully cited making the work verifiable even if there is disagreement in the ever-changing scene of botanical taxonomy. The detailed table of contents, many illustrations, and index are especially welcome.

This important volume should be essential for higher education curricula in the 21st century, especially in western North America. It should be required reading for any attempts at wetland restoration. "An Agreeable Landscape" sets a model for studies of desert river ecosystems anywhere in the world.—*Richard Felger, University of Arizona Herbarium, Tucson, Arizona, U.S.A.*

ENDOSPERM AND COTYLEDON AREOLE CORRELATION IN LEGUMINOSAE SUBFAMILY PAPILIONOIDEAE

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ABSTRACT

Cotyledon areoles are peculiar, often subtle, areas of cells of unknown function on the abaxial cotyledon surface of most papilionoid legume seeds. Previous research on a few tribes and analysis of generally ignored nineteenth-century literature suggested that cotyledon areoles are always associated with lateral endosperm deposits, which contain galactomannan energy reserves. Of 52 species examined, from all papilionoid legume tribes, 11 showed neither cotyledon areoles nor discernible endosperm, and 39 showed both cotyledon areoles and discernible endosperm. Two species, *Dupuya madagascariensis* and *Hypocalyptus sophoroides* were exceptional; each has abundant endosperm, but cotyledon areoles were either absent (*D. madagascariensis)* or questionably discernible (*H. sophoroides*). Therefore, this broad survey corroborates previous findings that cotyledon areoles are always absent when lateral endosperm deposits are absent, but indicates that cotyledon areoles are ordinarily, but not always, present when lateral endosperm deposits are evident. Cotyledon areole size is positively correlated with endosperm size. The correlation of presence or absence, position, and relative size of cotyledon areoles and endosperm, not previously reported, suggests an intertwined physiology and an unstudied role for cotyledon areoles in germination, which may have practical significance for many agricultural species, including the soybean, *Glycine max*. It also suggests that the taxonomic significance of cotyledon areoles is directly related to that of endosperm.

Key Words: antipit, pea, soybean, water relations; weathering resistance

RESUMEN

Las areolas del cotiledón son áreas de células peculiares, a menudo sutiles, de function desconocida situadas en la superficie abaxial del cotiledón de la mayoría de las semillas de las leguminosas papilionoides. Investigaciones previas en unas pocas tribus y el análisis de bibliografía del siglo diez y nueve generalmente ignorada sugieren que las areolas del cotiledón están siempre asociadas con depósitos laterales de endospermo, que contienen reservas energéticas de galactomanano. De 52 especies examinadas, de todas las tribus de leguminosas papilionoides, 11 no mostraron ni areolas del cotiledón ni endospermo apreciable, y 39 mostraron tanto areolas del cotiledón como endospermo apreciable. Dos especies, *Dupuya madagascariensis* y *Hypocalyptus sophoroides* fueron exceptionales; ambas tienen abundante endospermo, pero las areolas del cotiledón estaban ausentes (*D. madagascariensis)* o su apreciación era cuestionable (*H. sophoroides*). Sin embargo, esta amplia investigación corrobora hallazgos previos de que las areolas del cotiledón están siempre ausentes cuando los depósitos laterales de endospermo están ausentes, pero indica que las areolas del cotiledón están presentes normalmente, pero no siempre, cuando los depósitos laterales de endospermo son evidentes. El tamaño de la areola está correlacionada positivamente con el tamaño del endospermo. La correlación de presencia o ausencia, position, y tamaño relativo de las areolas del cotiledón y el endospermo, no presentados previamente, sugieren una fisiología entrecruzada y un papel no estudiado de las areolas del cotiledón en la germinación, que podría tener significado practico para muchas especies agrícolas, como la soja, *Glycine max*. También sugiere que el significado taxonómico de las areolas del cotiledón está directamente relacionado con el del endospermo.

Palabras Clave: antipit, guisante, soja, relaciones hídricas; Resistencia a la maduración

INTRODUCTION

Beck (1878) discovered a small peculiar characteristic spot "besondere Eigenthmülichkeit … Fleck," which he named an "Aleuronfleck" (protein-spot), on each abaxial cotyledon surface of dormant mature seeds of all studied species of legume tribe Vicieae DC. (= Fabeae Rchb.). At this spot, epidermal cells and subtending mesophyll cells contain chlorophyll-colored protein-containing bodies, and have different size and shape, stainability, pigmentation, and several distinctive anatomical and chemical characteristics compared with surrounding cells. In the soybean and other species of the genus *Glycine* Willd. (tribe Phaseoleae DC.), the spot, often subtle and known as a "pit" was rediscovered at least twice and has been studied extensively

(Dzikowski 1936, 1937; Miksche 1961; Yaklich et al. 1984, 1986, 1987, 1989, 1992, 1995, 1996, 1998; Baker & Minor 1987; Ma et al. 2004). All these soybean researchers thought that the "pit" was unique to the genus *Glycine*. Endo and Ohashi (1997) again rediscovered this spot in tribes Cicereae Alef., Trifolieae Endl., and Vicieae and named it a cotyledon areole, and later (Endo and Ohashi 1998a) established that the soybean "pit" is the same as their cotyledon areole. Endo and Ohashi (1998a, 1998b, 1999a, 1999b), found cotyledon areoles in 73% of studied species of Leguminosae Juss. subfamily Papilionoideae Giseke but absent in subfamilies Caesalpinioideae DC. and Mimosoideae DC. Presence in *Bobgunnia* J.H. Kirkbr. & Wiersema (tribe Swartzieae DC.), indicates that cotyledon areoles developed early in papilionoid evolution (Lackey 2009). Within the papilionoid legumes, presence or absence, shape, and position seem to have taxonomic significance for genera, tribes, and groups of tribes (Endo and Ohashi 1999a). Cotyledon areole function remains unknown (Ma et al. 2004; Lackey 2009).

Despite frequent statements to the contrary (Candolle 1825; Bentham 1865; Carlson & Lersten 2004), conspicuous endosperm deposits are found in most legume seeds (Schleiden & Vogel 1839b; Nadelmann 1890; Pammel 1899; Kopooshian 1963; Smith, 1983). These deposits almost always occur by lateral localized enlargement of endosperm tissue, which accommodates massive development of galactomannan, also known as gum or mucilage, secondary cell-wall material (Nadelmann 1890; Buckeridge et al. 2000). The relatively small lateral endosperm deposits of most modern soybean cultivars have been called an "antipit" (Ma et al. 2004). Presence or absence and degree of development seem to have taxonomic significance for species, genera, and tribes (Smith 1983). Studies of model legumes indicate that during germination, galactomannan is hydrolyzed to galactose and mannose, then transformed to sucrose in the endosperm, followed by transport to the cotyledons (Buckeridge et al. 2000).

Previous studies (Lackey 2007, 2008, 2009, 2010, unpublished results) of some tribe Phaseoleae, tribe Swartzieae, and other legumes suggested that cotyledon areole presence and position are always positively correlated with presence and position of conspicuous endosperm, as does an analysis of the results of Beck (1878) and Ma et al. (2004; et lit infra) for tribe Vicieae and *Glycine*. However, there is no broad survey to see if this correlation holds for all papilionoid legume tribes. The purpose of the current study is to examine at least one species from every papilionoid legume tribe in the systems of Polhill and Raven (1981), Polhill (1994a, 1994b) and Lewis et al. (2005) to verify that the correlation holds for all tribes. In addition, a substantial review is given of the extensive disconnected literature, particularly rarely-cited significant literature, of the last 200 years to see if current results shed any light on the function of cotyledon areoles and endosperm galactomannan, and thus the parallel systematic utility of these characteristics.

MATERIAL AND METHODS

At least one representative of all papilionoid tribes in the classification systems of Polhill and Raven (1981), Polhill (1994b), and Lewis et al. (2005) was examined. Included are the common commercial sources of papilionoid galactomannan gum: guar (*Cyamopsis tetragonoloba* (L.) Taub.) and fenugreek (*Trigonella foenum-graecum* L.). Specimens studied and results are given in Table 1.

Seeds were examined and stained by the methods of Lackey (2007, 2008). For those species with endosperm or cotyledon areoles, camera lucida outline drawings were made (Fig. 1), except for *Glycine max*, which is already well-depicted in the literature (Ma et al. 2004). Endosperm was considered present if seen with 50× optics and adjacent to any portion of the abaxial cotyledon surface. Minute endosperm residues between the cotyledon margins and the crease between the cotyledons and radicle, as well as any minutely thin remnants of the endosperm envelope surrounding the embryo were ignored. In this study, the term endosperm refers to visible lateral endosperm tissue unless designated otherwise. Approximate endosperm percent in cross section at the point of maximum occurrence was measured by the method of Anderson (1949). Cotyledon areoles were considered present if they were manifested by an unambiguously distinct spot of projecting epidermal cell walls on the cotyledon abaxial surface or a corresponding mirror-image impression on the endosperm, or if two or more of the following six cotyledon areole characteristics were present on the cotyledon abaxial side: 1) an area of epidermal cells along midvein of different size or shape than surrounding cells, 2) an area

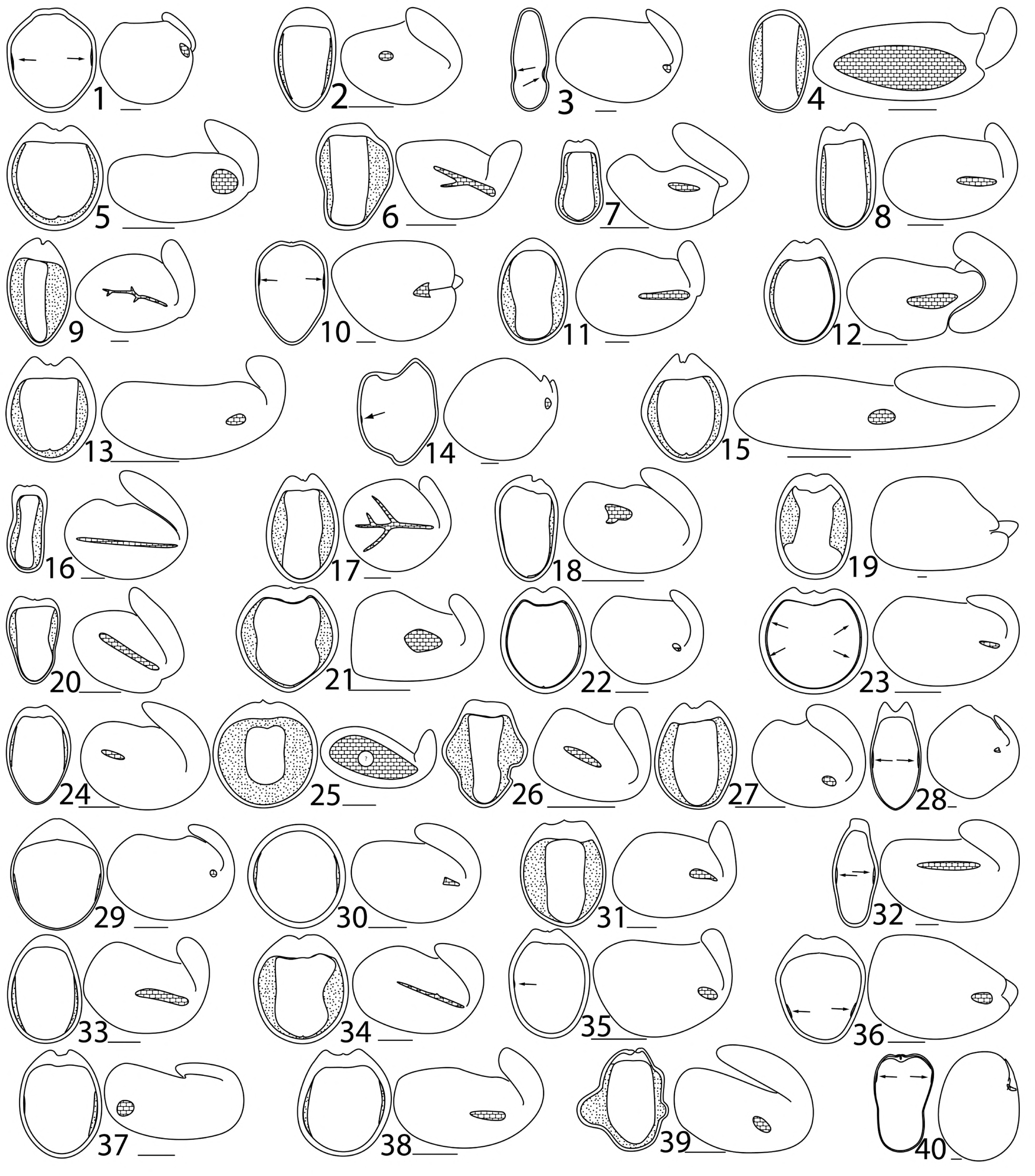

Fig. 1. Cotyledon areoles and endosperm in papilionoid legumes. Specimens lacking cotyledon areoles or endosperm are not drawn. For each specimen, a camera lucida drawing of a seed cross section outline is given. Any aril or epitesta are not shown. Lateral endosperm deposits are stippled. Small endosperm deposits are indicated by arrows. For each specimen, a left cotyledon and radicle is outlined. Cotyledon areoles are outlined and filled with a grid pattern.

(1) ***Abrus precatorius*** **L. (2)** ***Adesmia bicolor*** **(Poir.) DC. (3)** ***Ammopiptanthus mongolicus*** **(Maxim. ex Kom.) S.H. Cheng (4)** ***Amorpha fruticosa*** **L. (5)** ***Aotus ericoides*** **(Vent.) G. Don (6)** ***Apoplanesia paniculata*** **Presl (7)** ***Astragalus sinicus*** **L. (8)** ***Baptisia*** **sp. (9)** ***Bobgunnia madagascariensis*** **(Desv.) J.H. Kirkbr. & Wiersema (10)** ***Brongniartia canescens*** **(S. Watson) Rydb. (11)** ***Calpurnia aurea*** **(Aiton) Benth. (12)** ***Carmichaelia australis*** **R. Br. (13)** ***Chorizema cordatum*** **Lindl. (14)** ***Cicer arietinum*** **L. (15)** ***Securigera varia*** **(L.) Lassen (16)** ***Crotalaria cunninghamii*** **R. Br. (17)** ***Cyamopsis tetragonoloba*** **(L.) Taub. (18)** ***Desmodium discolor*** **Vogel (19)** ***Dupuya madagascariensis*** **(R. Vig.) J.H. Kirkbr. (20)** ***Genista stenopetala*** **Webb & Berthel. (21)** ***Glycine soja*** **Siebold & Zucc. (22)** ***Gompholobium scabrum*** **Sm. (23)** ***Goodia medicaginea*** **F. Muell. (24)** ***Hedysarum coronarium*** **L. (25)** ***Hypocalyptus sophoroides*** **(P.J. Bergius) Baill. (26)** ***Indigofera suffruticosa*** **Mill. (27)** ***Lotus maritimus*** **L. (28)** ***Lupinus luteus*** **L. (29)** ***Onobrychis conferta*** **(Desf.) Desv. (30)** ***Otholobium candicans*** **(Eckl. & Zeyh.) C.H. Stirt. (31)** ***Podalyria calyptrata*** **(Retz.) Willd. (32)** ***Pseudoeriosema borianii*** **(Schweinf.) Hauman (33)** ***Robinia pseudoacacia*** **L. (34)** ***Sesbania cannabina*** **(Retz.) Pers. (35)** ***Stylosanthes guianensis*** **(Aubl.) Sw. (36)** ***Templetonia retusa*** **(Vent.) R. Br. (37)** ***Tephrosia purpurea*** **(L.) Pers. (38)** ***Thermopsis villosa*** **(Walter) Fernald & B.G. Schub. (39)** ***Trigonella foenum-graecum*** **L. (40)** ***Vicia faba*** **L. Scale bars = 1 mm**

of epidermal cells that stain differently from surrounding cells, 3) a distinct green to yellow spot, 4) an area of epidermal cells lacking stomata, 5) an area with subepidermal cells of different size, shape, or stainability from surrounding cells, or 6) an area of epidermal cells with anticlinal walls sinuate parallel to the embryo axis.

RESULTS

Of the 52 species examined, 11 lacked cotyledon areoles and discernible endosperm, and 39 showed both cotyledon areoles and discernible endosperm. *Dupuya madagascariensis* (R. Vig.) J.H. Kirkbr. and *Hypocalyptus sophoroides* (P.J. Bergius) Baill. have abundant endosperm, but cotyledon areoles were either absent (*D. madagascariensis*) or questionably discernible (*H. sophoroides*). In all specimens, the maximum extent of lateral endosperm was always immediately external to the cotyledon areole (Table 1, Figs. 1–2).

Cotyledon areole position, size, shape, and other attributes varied from species to species (Table 1). Many were basal to medial. *Hedysarum coronarium* L. and *Tephrosia purpurea* (L.) Pers. were apical or subapical. All were positioned external to the midvein or when branched (Fig. 2s), external to the midvein and portions of major branch veins. Size and shape varied from minute to perhaps almost a third of the cotyledon surface (*Amorpha fruticosa* L., Fig. 2u), from oval to linear, and from unbranched to branched. Within *Glycine*, the wild soybean, *G. soja* Siebold & Zucc., had a much larger cotyledon areole, relative to overall seed size, than the cultivated soybean, *G. max* (L.) Merr. Cotyledon areole epidermal cells differed in size and shape from other cotyledon epidermal cells (Fig. 2h, 2t). In some species and some seeds of some samples, cotyledon areole epidermal cells were slightly green-yellow or a slightly darker color relative to most other cotyledon epidermal cells (Fig. 2g, 2l). Sometimes the cotyledon areole was in a localized concave area (Fig. 2g, 2n) filled with corresponding endosperm tissue (Fig. 2g, 2o). Most species had no such concave area. Cotyledon areole epidermal cells almost always had convex outer periclinal walls, which gave a shagreened or granular appearance when viewed under low magnification and lateral bright light (Fig. 2e, 2n). The anticlinal walls parallel to the cotyledon axis were often sinuate in surface view (Fig. 2t). The cotyledon areole epidermal cells usually stained less readily with surface-applied toluidine blue than other cotyledon epidermal cells (Fig. 2f, 2l, 2r). Cotyledon mesophyll cells between the cotyledon areole epidermal cells and the veins usually stained more readily with toluidine blue than other mesophyll cells outside the cotyledon areole, and cell size and position were different from other mesophyll cells (Fig. 2m). In embryos hydrated after removal from the endosperm envelope, epidermal blistering of epidermal cells outside the cotyledon areole was generally greater, but sometimes lesser, than the minimal epidermal blistering occurring in embryos hydrated while still within the endosperm envelope. Cotyledon areole cell size and shape and other epidermal features could often be seen readily as a mirror-image impression on the interior surface of dry endosperm tissue (Fig. 2n, 2o). Many times this impression gave a better surface view of the cotyledon areole appearance than the direct view of the cotyledon.

Endosperm extent varied from unobservable with 50× optics to occupying 60% of seed width (Fig. 2q). When visible, it always formed a complete envelope around the embryo (Fig. 2d) and always adherent to the testa. It was almost always free from, rarely adherent to, the embryo. The embryo outline (Fig. 2b) and the most minute details of the embryo epidermis could be seen as impressions on the dry endosperm interior. Thickness of the endosperm envelope was not uniform, but varied according to a consistent layout. It was thinnest under the hilum. A slight thickening occurred in the triangular (in cross section) slit formed where the cotyledon margins touch (Fig. 2i). At a similar, but usually larger, slit between the radicle and cotyledons a somewhat larger deposit formed (Fig. 2b). The greatest development, if any, occurred adjacent to the abaxial cotyledon faces (Fig. 2a). The development of this area varied in position to be directly exterior to the cotyledon areole. It was usually more or less symmetrically positioned about the cotyledon areole, but sometimes it was slightly asymmetrically positioned towards the apex of the cotyledon, especially if the cotyledon areole was basal. Hardness of the endosperm to a knife or cutters varied from relatively soft to fairly hard (*Cyamopsis tetragonoloba*), but always softer than the dry Malpighian layer of the testa. It was usually colorless, sometimes dark to red-purple (*Vicia faba* L.), and generally appeared crystalline when cut. When well-developed, three layers of endosperm could generally be seen. The outer aleurone layer was

Table 1. Cotyledon areole and endosperm presence in papilionoid legumes. Tribes are those of Lewis et al. (2005). New reports for cotyledon areoles are indicated by an asterisk before a species name. Endosperm percent is a ratio of both lateral endosperm deposits compared to seed width. Cotyledon areole presence or absence is indicated either by noCa, or by position codes from Endo and Ohashi (1999a): B=basal, BM=basal medial, M=medial, MA=medial apical, A=apical, ?=presence questionable. Specimens source data are given after author's (JAL) accession number.

Species	CA/noCA	Endo %	Tribe	Specimen
Abrus precatorius L.	B	2	Abreae	JAL1168 USA Commercial lot Banana Tree 10 Sep 2004
**Adesmia bicolor* (Poir.) DC.	M	3	Dalbergieae	JAL1620 Uruguay PI 138776 B Rosengurtt (BARC)
**Ammopiptanthus mongolicus* (Maxim. ex Kom.) S.H. Cheng	B/M	2	Thermopsidieae	JAL1650 China Arb Chinese Acad Forestry, Peking 1950 #34 41N 107E 1000m (BARC)
Amorpha fruticosa L.	B-MA	30	Amorpheae	JAL1613 USA bulk collection (BARC)
**Aotus ericoides* (Vent.) G. Don	B	10	Mirbelieae	JAL1638 Krukoff list 74 ship 23 (BARC)
**Apoplanesia paniculata* Presl	B-MA	30	Amorpheae	JAL1612 Mexico Ripley & Barneby 14833 26 Nov 1967 (US) (BARC)
Arachis monticola Krapov. & Rigoni	noCa	noEndo	Dalbergieae	JAL1618 Argentina PI 219824 (BARC)
**Astragalus sinicus* L.	M	30	Galegeae	JAL1621 Japan SPI 6330 Tokyo (BARC)
**Baptisia* sp.	B-BM	10	Thermopsidieae	JAL1178 USA Lackey Cultivated, Botanic Gardens, Washington, DC 12 Sep 2004
Bobgunnia madagascariensis (Desv.) J.H. Kirkbr. & Wiersema	B-A	50	Swartzieae	JAL1600 Togo Ern 2652a Zwischen Sokode und Aleheride (BARC) 8 Dec 1977(B)
**Brongniartia canescens* (S. Watson) Rydb.	B	2	Brongniartieae	JAL1631 Mexico C.H. Muller 3339 Chihuahua (BARC)
**Calpurnia aurea* (Aiton) Benth.	B-BM	45	Podalyrieae	JAL1643 Krukoff list 35, A. Bell rec Apr 1977 (BARC)
Carmichaelia australis R. Br.	M	8	Galegeae	JAL1625 Australia Coll 1984 RBG Melbourne (BARC)
**Chorizema cordatum* Lindl.	B	15	Mirbelieae	JAL1639 Krukoff list 82 A. Bell rec Apr 1977 (BARC)
Cicer arietinum L.	B	1	Cicereae	JAL1622 USA Lackey Commercial lot Patels 17 Jun 2007
Cladrastis kentukea (Dum. Cours.) Rudd	noCa	noEndo	Sophoreae	JAL1181 USA Lackey Cultivated Virginia as *Cladastrus lutea* 26 Sep 2004
**Crotalaria cunninghamii* R. Br.	B-A	35	Crotalarieae	JAL1649 Australia Jackson 2953 W Jackson White Springs Ruins 21 Aug 1977 (BARC)
Cyamopsis tetragonoloba (L.) Taub.	B-A	60	Indigoferae	JAL1583 NPGS PI 250357 15-Dec-2006
**Dalbergia retusa* Hemsl.	noCa	noEndo	Dalbergieae	JAL1169 Lackey Commercial lot Banana Tree 10 Sep 2004
**Desmodium discolor* Vogel	M	10	Desmodieae	JAL1409 PI 319466 (BARC)
**Dipteryx punctata* (S.F. Blake) Amshoff	noCa	noEndo	Dipteryxeae	JAL1608 British Guiana Smith 3164 (V) (BARC)
**Dupuya madagascariensis* (R. Vig.) J.H. Kirkbr.	noCa	50	Swartzieae	JAL1601 Madagascar Capuron s.n. (BARC)
**Euchresta horsfieldii* (Lesch.) Benn.	noCa	noEndo	Euchresteae	JAL1647 Philippines D.R. Mendoza 18484 Luzon May–Jun 1953(BARC)
**Genista stenopetala* Webb & Berthel.	B-A	30	Genisteae	JAL1653 Canary Islands G.V. Perez FPI 42574Tenerife, CI (BARC)
Glycine max (L.) Merr.	M	15	Phaseoleae	JAL1598 China NPGS PI 68728 1 May 2007
Glycine soja Siebold & Zucc.	M	30	Phaseoleae	JAL94 NPGS PI 342618B (BARC)
**Gompholobium scabrum* Sm.	B	10	Mirbelieae	JAL1641 Krukoff list 61 as *Burtonia scabra* (BARC)

Table 1. continued.

Species	CA/noCA	Endo %	Tribe	Specimen
**Goodia medicaginea* F. Muell.	B	3	Boissaeeae	JAL1635 BM carpology (BARC)
Hedysarum coronarium L.	A	7	Hedysareae	JAL1627 Algeria SPI 3959 Dr. L. Trabut (BARC)
**Hypocalyptus sophoroides* (P.J. Bergius) Baill.	?	65	Hypocalypteae	JAL1645 Krukoff list 45 ship 8 CRG 2/24/76 (BARC)
Indigofera suffruticosa Mill.	M-MA	40	Indigoferae	JAL1615 IND16 No.1156 (BARC)
**Lespedeza bicolor* Turcz.	noCa	noEndo	Desmodieae	JAL1310 PR 1693 (BARC)
**Lotus maritimus* L.	B	40	Loteae	JAL1616 Bereich Botanik und Arboretum (BARC)
Lupinus luteus L.	B	3	Genisteae	JAL1199 Lackey Commercial lot Mediterranean Bakery 20 Apr 2005
**Onobrychis conferta* (Desf.) Desv.	B	3	Hedysareae	JAL1629 Hort Bot Leningrad as *Onobrychis argentea* Boiss. (BARC)
**Otholobium candicans* (Eckl. & Zeyh.) C.H. Stirt.	B	3	Psoraleeae	JAL1335 RSA PI 184376 (BARC)
**Podalyria calyptrata* (Retz.) Willd.	B-M	55	Podalyrieae	JAL1644 Krukoff list 33 A. Bell rec Apr 1977 (BARC)
**Pseudoeriosema borianii* (Schweinf.) Hauman	M	4	Phaseoleae	JAL267 CSIRO CPI 52399
Robinia pseudoacacia L.	B-M	15	Robinieae	JAL1442 USA Allen IP 8110 (BARC)
**Securigera varia* (L.) Lassen	M	20	Loteae	JAL1654 France FPI 19703 Paris (BARC)
Sesbania cannabina (Retz.) Pers.	BM-MA	40	Sesbanieae	JAL1443 Ceylon FPI 80148 (BARC)
**Sophora secundiflora* (Ortega) Yakovlev	noCa	noEndo	Sophoreae	JAL1652 Soil Cons. Serv T-2321as *Calia secundifolia* (BARC)
Sophora tomentosa L.	noCa	noEndo	Sophoreae	JAL1607 Mexico Andrews Yu23A, B (US) (BARC)
**Stylosanthes guianensis* (Aubl.) Sw.	B	1	Dalbergieae	JAL1619 PI 339898 (BARC)
Swartzia apetala Raddi	noCa	noEndo	Swartzieae	JAL1221 Brazil Callejas et al.1690 (US)
Swartzia sp.	noCa	noEndo	Swartzieae	JAL1605 Krukoff 67 from Bell Apr 1977 (BARC)
**Taralea oppositifolia* Aubl.	noCa	noEndo	Dipteryxeae	JAL1610 Brazil Jose Maria de Albuquerque coll 1989 (BARC)
**Templetonia retusa* (Vent.) R. Br.	B	3	Brongniartieae	JAL1637 Krukoff list 38 A. Bell rec Apr 1977 (BARC)
Tephrosia purpurea (L.) Pers.	A	5	Millettieae	JAL1614 India PL480 Project A7CR284 Coll no 2648 26 Mar 1975 (BARC)
**Thermopsis villosa* (Walter) Fernald & B.G. Schub.	M	10	Thermopsidieae	JAL1651 PR 1469 as *Thermopsis caroliniana* (BARC)
Trigonella foenum-graecum L.	*B*	*50*	*Trifolieae*	*JAL1553 USA Lackey Grocery store* 1 Jan 2006
Vicia faba L.	B	1	Fabeae	JAL1002 USA Lackey Commercial lot Mediterranean Bakery 24 Jul 2004

usually barely visible with 50×. The middle layer, if developed to any degree, could be seen as a crystalline mass with cell patterns radiating out from the seed center. Cell diameter was about 20 microns in *Trigonella foenum-graecum* and *Glycine max*, and, when observed, remaining species were comparable. The inner layer was denser, and more solidly crystalline, than the middle layer. Upon wet dissection the endosperm took water readily and formed a complete envelope of slick material allowing easy removal of the embryo. In hot water, gum left the endosperm tissue and formed a clear, generally colorless, thin gel, which dried to form a thin, strongly adherent, layer on glass surfaces. Endosperm of seeds left to hydrate, could be seen to protrude turgidly from cracks in the testa (Fig. 2c). Endosperm of *Glycine* (Fig. 3) was unexceptional relative to other

species. The wild soybean, *G. soja*, had endosperm larger than average (Anderson 1949; current results) for papilionoid legumes. The cultivated soybean, *G. max*, had a much smaller than average endosperm.

Although often subtle, detection of cotyledon areoles and endosperm was usually immediately unambiguous, but several specimens presented problems. Detection generally seemed easiest for compact or even small cotyledon areoles that showed a clear differentiation from remaining cotyledon epidermal cells. Very small seeds, very small cotyledon areoles, or very large cotyledon areoles made observation difficult. *Ammopipthanthus mongolicus* (Maxim. ex Kom.) S.H. Cheng and *Stylosanthes guianensis* (Aubl.) Sw. were difficult to dissect, and had small cotyledon areoles and endosperm, near the limit of detection. *Lespedeza bicolor* Turcz. likewise was difficult to dissect, and any cotyledon areole or endosperm were too small to allow unambiguous detection. *Amorpha fruticosa* had a large endosperm, and the presumptive cotyledon areole appears large, covering much of the abaxial surface (Fig. 2u); in cross section, the usual disruption of mesophyll cell patterns below the cotyledon areole is not readily evident, but these mesophyll cells do stain more readily than adjacent ones (Fig. 2m). Similarly, *Hypocalyptus sophoroides* had massive white endosperm, but a cotyledon areole was not readily conspicuous, although a patch of larger cells with slightly protruding periclinal exterior walls over the middle vein suggests a cotyledon areole, but with no clear distinction and no differential staining from the remaining smaller epidermal cells (Fig. 2t); in cross section through the cotyledon base, mesophyll is entirely spongy, with no readily apparent distinction in the cotyledon areole area. *Dupuya madagascariensis* was the only species with a conspicuous prominent endosperm and no indication of cotyledon areole.

Cotyledon areole size seemed generally positively correlated with endosperm size. The correlation was demonstrated by measurement. Cotyledon areole length relative to cotyledon length ranged from 0.06 (*Cicer arietinum* L.) to 0.82 (*Crotalaria cunninghamii* R. Br.). In those species with cotyledon areoles, there was a positive correlation between cotyledon areole relative length and relative endosperm thickness (R^2=0.35).

DISCUSSION

Correlation

Results of the current broad sampling of all papilionoid legume tribes, concurs with previous work in specific groups to show an almost perfect positive correlation between cotyledon areole presence and position and endosperm presence and position in papilionoid legumes. The only known exception, discovered in the current work, is the absence of a cotyledon areole in *Dupuya madagascariensis*, where abundant endosperm is found. A similar possible exception is *Hypocalyptus sophoroides*.

Although prior authors did not note any correlation, a review of their observations in specific groups supports it. In Vicieae, analysis of Beck's (1878) purely descriptive anatomical work indicates that basal cotyledon areoles are always present and positioned adjacent to endosperm in all studied species of *Vicia*, and noted for the genera *Pisum*, *Lens*, and *Lathyrus,* for which he cited no species. Yaklich et al. (1989) observed medial cotyledon areoles and what is now known to be adjacent endosperm in all 185 accessions of soybean and 45 accessions of seven other species of *Glycine* (tribe Phaseoleae subtribe Glycininae Benth.). Additional support is in Phaseoleae subtribe Clitoriinae DC., in which Lackey (2007) found cotyledon areoles and endosperm in all studied species of *Periandra* Mart. ex Benth., *Centrosema* (DC.) Benth., and *Barbieria* DC., and two species of *Clitoria* L., but no cotyledon areoles and no endosperm in four *Clitoria* species. In Phaseoleae subtribe Kennediinae Benth., Lackey (2008) found cotyledon areoles and prominent endosperm in all studied species. Lackey (2009) found cotyledon areoles and endosperm in *Bobgunnia madagascariensis*, and no cotyledon areoles or endosperm in two *Swartzia* species (tribe Swartzieae). Lackey (2010) found both endosperm and cotyledon areoles in *Pueraria montana* (Lour.) Merr. and *Cyamopsis tetragonoloba*.

Across the range of papilionoid legumes with cotyledon areoles studied here, in addition to the above described correlation with endosperm presence or absence and position, cotyledon areole size, as measured by length along the midvein, was positively correlated with endosperm size, when adjusted for seed size differences. Lackey (2010) found a similar positive size correlation across a range of wild, semiwild, and domesticated soybean samples, which are a single interbreeding gene pool.

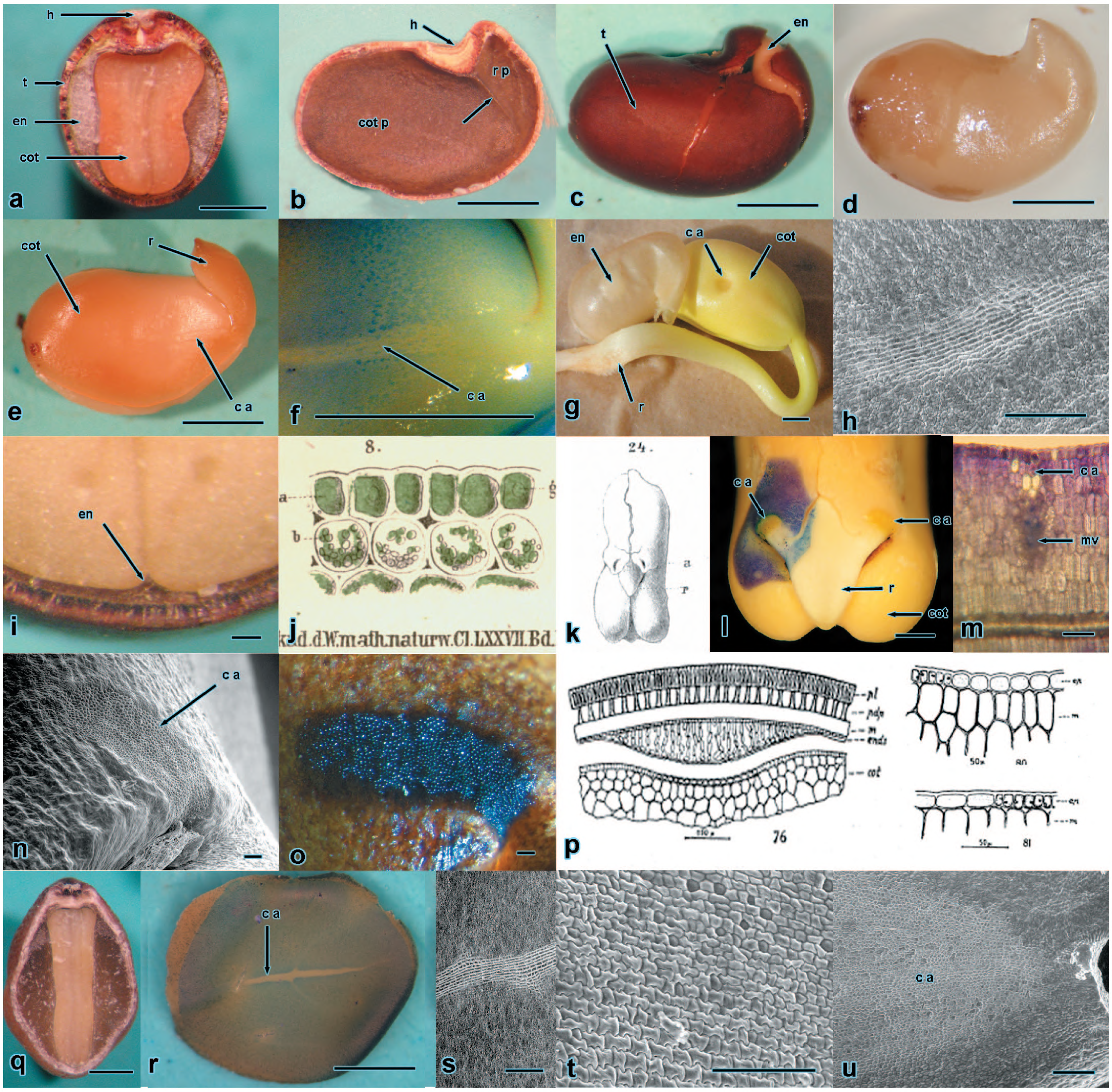

Fig. 2. Cotyledon areoles and endosperm in papilionoid legumes.

(**a**) *Sesbania cannabina* (Retz.) Pers. JAL 1443. (**b–f**) *Robinia pseudoacacia* L. JAL 1442. (**g**) *Glycine max* (L.) Merr. JAL 1598. (**h**) *Indigofera suffruticosa* Mill. JAL 1615. (**i**) *Goodia medicaginea* F. Muell. JAL 1635. (**j–k**) *Vicia faba* L. lithograph figures 8, 24 from Beck (1878). (**l**) *Vicia faba* L. JAL 1002. (**m**) *Amorpha fruticosa* L. JAL 1613. (**n–o**) *Vicia faba* L. JAL 1002. (**p**) *Glycine max* (L.) Merr. lithograph figures 76, 80, 81 from Dzikowski (1937). (**q**) *Cyamopsis tetragonoloba* (L.) Taub. JAL 1582. (**r–s**) *Cyamopsis tetragonoloba* (L.) Taub. JAL 1585. (**t**) *Hypocalyptus sophoroides* (P.J. Bergius) Baill. JAL 1645. (**u**) *Amorpha fruticosa* L. JAL 1613.

(**a**) Transverse dry seed section. Conspicuous endosperm in two large lens-shaped areas on each abaxial side of cotyledons. (**b**) Median dry seed section, embryo removed. Interior of testa lined with adherent endosperm, showing endosperm thickening ridge (at uncaptioned arrow) formed between radicle and cotyledon pockets. (**c**) Exterior hydrated seed, left side. Cracks around hilum and radicle, showing endosperm beneath cracks in testa. (**d**) Endosperm envelope, hydrated, from (c). Embryo removed. (**e**) Embryo, hydrated, from (c). Faint reflections from cotyledon areole epidermal cells. (**f**) Embryo, hydrated and stained with toluidine blue, from (c), Staining lighter at cotyledon areole than remaining cotyledon surface. (**g**) Germinating seed on germination paper, shedding the testa and adherent endosperm. Matching cotyledon areole/endosperm pair. Cotyledon areole is yellow-green. Endosperm shows through semi-transparent testa. (**h**) Cotyledon dry abaxial surface, SEM. Distinct cotyledon areole. (**i**) Transverse dry seed section. Endosperm thickening at margins of cotyledons. (**j**) Cotyledon areole ("Aleuronfleck") in cross section (300X), *a* large granules ("Körner") of the epidermis, *b* smaller granules of the parenchyma, *g* globoids ("Globoide"). Note large and smaller granules are hand-tinted yellow-green (Pantone 366 U) in original figure. External periclinal epidermal cell walls slightly convex. (**k**) Ventral view of hulled seed of *Vicia faba*, *r* radicle ("Radicula"), *a* cotyledon areole ("Aleuronfleck"). (**l**) Embryo, dry, stained on one side with toluidine blue. Cotyledon areole is yellow-green, stains less readily than surrounding cotyledon area. (**m**) Transverse section of cotyledon through cotyledon areole and midvein. (**n**) Cotyledon areole, SEM. (**o**) Endosperm from same seed

Fig. 3. Transverse seed section of semiwild soybean (*Glycine gracilis* Skvortsov PI 86046 from Hokkaido, Japan. Many other landraces, wild, and semiwild soybeans are similar with galactomannan-containing endosperm appearing as a lens-shaped crystalline structure on each side of the cotyledons. Most US soybean cultivars lack such a well-developed endosperm. The endosperm is a potential source for commercial galactomannan gum.

Problem observations

Most observations of cotyledon areoles in Table 1 are new. Nineteen confirm previous literature reports. Most observations are unambiguous. However, two contradict previous observations: *Indigofera suffruticosa* and *Amorpha fruticosa* are reported here with a cotyledon areole, but Endo and Ohashi (1999a) report no cotyledon areole. The first species has small seeds that are difficult to observe, but nonetheless show unambiguous cotyledon areole (Fig. 2h). As discussed in results, detection of the cotyledon areole of *Amorpha*

in (n), unstained and natural color. Endosperm dark pigmented. (p) 76. Seed coat with lenticular formation ("formation lenticulaire") of the endosperm and adjacent cotyledon. Transverse section in glycerin. *pl* palisade tissue ("couche en palissade"), pdp hourglass layer ("cellules auxiliaires"), *m* parenchyma tissue ("couches du parenchyme"), *ends* endosperm remnants with lens ("lenticule")between aleurone tissue and parenchyma, *cot* cotyledon. 80. Cotyledon abaxial surface below the endosperm lens ("lenticule"). Transverse section. *ep* epidermis, *m* parenchyma. 81. As figure 80, Longitudinal section. Note Dzikowski's depiction of cotyledon areole epidermal cells with convex periclinal walls in figure 80. Also note the cotyledon areole epidermal cells width greater than surrounding cells in figure 80 and smaller in figure 81. (q) Transverse dry seed section. Massive hard endosperm on each abaxial side of cotyledons. (r) Embryo, dry, stained with toluidine blue. Staining lighter at cotyledon areole. (s) Cotyledon areole, SEM. Branching at lateral veins. (t) Cotyledon surface, SEM. Cotyledon areole epidermal cells in lower left show elongated cells with sinuate anticlinal longitudinal walls. Remaining cotyledon epidermal cells in upper right show more isodiametric cells with no such sinuate walls. (u) Cotyledon surface, SEM. Large cotyledon areole contrasts with remainder of cotyledon surface on periphery.

c a = cotyledon areole, cot = cotyledon, cot p = cotyledon pocket, en = endosperm, h = hilum, mv = midvein, r = radicle, r p = radicle pocket, t = testa. Abbreviations and translated description for (j, k, p) follow Beck (1878) and Dzikowski (1937). Scale bars = 100 µm in h–i, m–o, s–u 1 mm in all others.

fruticosa is problematical. As with *Hypocalyptus sophoroides*, the endosperm in *A. fruticosa* is very large, and the presumed cotyledon areole is also very large, covering most of the cotyledon abaxial surface, thus not presenting a clear distinction between cotyledon areole epidermal cells and surrounding epidermal cells (Fig. 2u). The difficulty of false negative reports for cotyledon areoles has been noted previously (Lackey 2008; Yaklich et al. 1989) for initial survey studies that were later followed by in-depth anatomical work, particularly when seeds and cotyledon areoles are small. The same difficulty seems to occur when cotyledon areoles appear to cover most of the cotyledon surface. Current results confirm the occasional difficulty of detecting cotyledon areoles in some species, and both current discrepancies with the literature seem to conform with this known problem. The most readily distinctive cotyledon areoles seem to be in those specimens with relatively large seeds, average to small endosperm, and relatively small cotyledon areoles, such as the *Vicieae* and *Glycine* spp., the very species in which the cotyledon areoles were first discovered. Detection of lateral endosperm deposits was even less ambiguous than cotyledon areoles. However, absent exhaustive observation, it may sometimes be possible to overlook small endosperm deposits if they are localized and near the cotyledon base or apex.

Integration with prior literature

To combine current results with past findings, requires a preliminary literature summary that is necessarily lengthy, despite all attempts at brevity. The combination with recent literature (Endo & Ohashi 1998a, 1998b, 1999a, 1999b; Ma et al. 2004; Lackey 2007, 2008, 2009, 2010) and long-overlooked anatomical findings (Schleiden & Vogel 1839b; Beck 1878), indicate a need to reassess some basic questions regarding the structure and function of cotyledon areoles and endosperm in papilionoid legumes, and any possible selective advantage.

Cotyledon areole structure

Three independent sources form the basis for detailed understanding of cotyledon areole anatomy: Beck's (1878) comparative anatomy of mature dormant Vicieae seeds, Ma et al.'s (2004) anatomical study of mature dormant and germinating soybean seeds, and Endo and Ohashi's (1997, 1998a, 1998b, 1999a, 1999b) treatments on developing, dormant, and germinating seeds of many papilionoid legumes. The three results have never been combined. None of these authors knew of each others work at the times of publication (Yasuhiko Endo & Fengshan Ma, pers. comm. 2009), however, Endo and Ohashi (1998a) and Ma et al. (2004) both knew about Miksche's (1961) brief description of the cotyledon areole in soybean. Ma et al. (2004) also referenced a substantial body of work on soybean cotyledon areoles (Dzikowski 1936, 1937; Yaklich et al. 1984, 1986, 1987, 1989, 1992, 1995, 1996, 1998; Baker & Minor 1987). Despite their varied scope and emphasis, and lack of awareness of each other's work, the overlapping areas of these three sources present a generally consistent description of the cotyledon areole, with variation from taxon to taxon and even from cultivar to cultivar within a species. In some taxa, some attributes appear to be completely missing. The three sources combined with Lackey (2007, 2008, 2009, 2010) characterize the cotyledon areole as a slightly dark, greenish or yellow-green, oval to linear, protein body containing spot on each abaxial cotyledon epidermis, above the midvein, sometimes branched, and sometimes in a depression. Cotyledon areole epidermal cells are usually larger, sometimes smaller, but always differ in size and shape from other cotyledon abaxial epidermal cells, do not form stomata, and have strongly convex outer periclinal walls which give a "granular" appearance to the cotyledon areole surface. In surface view, the anticlinal walls parallel to the cotyledon axis are often "wavy" (Ma et al. 2004) or sinuate parallel to the cotyledon midvein. The cotyledon areole epidermal cell walls have thicker outer periclinal walls and cuticle, and stain less readily than surrounding epidermal cells. Each cotyledon areole epidermal cell contains one large proteinaceous, chlorophyll-colored body, or "Aleuronkorn" (Beck 1878). Mesophyll cells between the cotyledon areole epidermal cells and the midvein are generally smaller than other mesophyll cells and contain several smaller similar bodies or "Körner" (Beck 1878), "granules" or "structures" (Endo & Ohashi 1999b). In alcohol, chlorophyll is extracted from these chloroplasts more slowly than from others in the cotyledon, leaving a yellow-green, and eventually a red-brown pigment. The cotyledon areole appears during late stages of seed development, reaches its full

expression in the mature dormant seed, and the plastids and other internal and external cell structures degenerate upon germination. In a summary article, Endo and Ohashi (2010) proposed the Japanese name ‘Shiyômon’ for the cotyledon areole.

The current research conforms with the above description and adds differential imbibition damage at the cotyledon areole compared with the remaining adaxial cotyledon epidermis. The current research confirms prior suggestions (Lackey 2009, 2010) that cotyledon areole presence and position is correlated with endosperm presence and position.

Most of the literature is ambiguous as to whether the cotyledon areole refers to a cotyledon surface feature, and therefore merely the epidermal cells, or also includes the internal cotyledon cells between the epidermis and midvein. It seems more useful to define the cotyledon areole in the broader sense, which would include both the specialized epidermal cells and specialized cotyledon mesophyll cells, and this broader definition is used here.

Endosperm structure

The structure of legume endosperm in the mature dormant seeds has been studied longer and in more detail than the structure of cotyledon areoles. A huge body of significant 19th century anatomical work, beginning with Bronn’s (1822) detailed findings, is almost never cited now, and with trivial exception has never been compared with recent findings. At least since perhaps Schleiden (1838) and Schleiden and Vogel (1839a, 1839b) legume endosperm has two well-known functions with corresponding structures. In the mature dormant seed it acts as a polysaccharide energy reserve for germination (Buckeridge et al. 2000), but in early developmental stages it supplies nourishment of the developing embryo (Chamberlain et al. 1993). Developmental structures of the second endosperm function are outside the current study and will not be reviewed.

In a remarkable, and strangely, seemingly modern work, the anatomical treatment of endosperm, or albumin, by Schleiden and Vogel (1839b), carried out with the most rudimentary optical and mechanical instruments (Schleiden 1849), and unfortunately rarely cited now, is an expansion of their parenthetic treatment during their classic study of legume floral development (Schleiden and Vogel 1839a), and remains the most comprehensive, and in many instances the most detailed, legume endosperm study to date. They established, by means of development studies and anatomical examination of almost 300 different legume seeds, many basic facts. First, the albumin of legumes is endosperm, i.e. of embryo sac origin, and not perisperm, i.e. of nucellar or maternal origin. Also, the endosperm consists of cells, in accord with Schleiden’s (1838) cell theory. They found that, contrary to common statements (Candolle 1825), endosperm is widespread and often well-developed in legumes. Although often well-developed, it can be reduced to a greater or a lesser degree, which in their opinion is caused by an enlarged embryo, which displaces and compresses the endosperm. The endosperm development is generally greatest on the sides of the cotyledons, least on the cotyledon margins and under the hilum in subfamily Papilionoideae, and most persistently present in the slit between radicle and cotyledons. The material of the endosperm walls is gelatinous or mucilaginous, transparent, swells in water, particularly hot water, is tasteless, and is harder in Caesalpinioideae and Mimosoideae than in Papilionoideae. They described the anatomy of the tissue layers of endosperm in detail, which when fully developed, consists of three layers. Although the details varied considerably in such a vast family, exterior is the first tissue layer, usually a single row of regular cells with distinct cell contents, now called the aleurone layer (Pammel 1899). A second or middle tissue layer consists of a few to many cell layers, which is the chief constituent of the endosperm. The individual secondary cell walls are filled with mucilage, to the extent that in some cells, the lumen may almost disappear. The cells are of many shapes, but often elongated with the long axis towards the embryo, and are often arranged in radiating patterns with the embryo as the center. The mucilage seems to be deposited in the secondary cell walls in layers, the mucilage layer nearest the lumen sometimes denser, and is often traversed by pore canals to the primary cell wall. The third or innermost endosperm tissue layer consists of a few layers of cells that are similar to the middle layer, and sometimes intergrade with it, but are crushed by pressure of the immediately interior cotyledon

epidermis, and it is this third layer that is seen when only a thin layer of endosperm remains. Later research (Sempolowski 1874; Chalon 1875; Beck 1878; Avetta 1884; Nadelmann 1890; Pammel 1899; Smith 1981, 1983; Meier & Reid 1977) has clarified, extended, confirmed and updated Schleiden and Vogel's (1839b) above summarized basic results about legume endosperm to conform with advances in basic biological theory, but never contradicted it to any significant degree, with the exception of their theory of endosperm reduction caused by embryo expansion.

The complex method of mucilage deposition in the secondary cell walls (Dhugga et al. 2004) was studied by Nadelmann (1890) by light microscopy for many legume species and Meier and Reid (1977) by TEM in fenugreek, *Trigonella foenum-graecum*. Both confirmed Schleiden and Vogel's (1839b) observations that mucilage is deposited in secondary cell walls, i.e. cell walls that are formed after the cells have stopped enlarging, and both reported deposition from vesicles formed within the cells. Meier and Reid (1977) show in their figures 2 and 8, TEM photographs of endosperm cells before and after deposition of about 20 microns broad, about the same as seen in the current study, although under different preparation protocols. Although without scale indication, Nadelmann (1890) presents cell line drawings in three stages of deposition, which indicate no apparent cell enlargement. This confirms prior observations that mucilage deposition, or lack thereof, has no effect on increasing endosperm cell size, but merely is accommodated by the pre-determined cell size. Both works also confirm centripetal step-wise deposition of mucilage in layers, starting with a position adjacent to the middle lamella and proceeding inward, towards the lumen; the space occupied by the mucilage causes a reduction in lumen size, finally resulting in a very small, sometimes almost non-existent lumen, and possible cell death, with few remnants of cell contents. However Ma et al. (2004) report these mature endosperm cells as still living in soybean, as do Tonini et al. (2006) for *Sesbania virgata*.

Anatomical findings in the current study conform with endosperm structure described above. Endosperm is always found as a complete, although often very thin, envelope around the embryo, and is always visible as a minute enlargement at the cotyledon margins and in the slit between radicle and cotyledons. When prominent, it is always by enlargement on the lateral embryo sides, occasionally quite small and distinct, as seen here in *Vicia faba*, and previously observed by Beck (1878) in tribe Vicieae and Bronn (1822) in pea (*Pisum sativum*). Sometimes it occupies most of the seed, as in *Hypocalyptus sophoroides*. The material is dense, almost crystalline, occasionally dark colored, and dissolves in water.

Endosperm in *Glycine* was visually unexceptional relative to other legumes, and in the wild and semiwild soybeans seen here (*G. soja* and *G. gracilis* Skvortz., Fig. 3), endosperm was substantial. The descriptive endosperm results of Ma et al. (2004), although describing a small lateral endosperm deposit, given the unique name "antipit" in the cultivated soybean, are likewise unexceptional relative to other endospermic legumes.

Endosperm function

The chemical structure and physiology of the endosperm mucilage has been subject to extensive study because of its pervasive commercial importance in petroleum extraction, food, cosmetics, pharmaceuticals, textiles, paper, and a wide variety of industrial uses (Buckeridge et al. 2000). Although potentially available from a variety of legume species (Tookey & Jones 1965), current primary commercial sources are guar (*Cyamopsis tetragonoloba*), locust (*Ceratonia siliqua* L.), and fenugreek (*Trigonella foenum-graecum*). All of which are subject to supply and price uncertainties, and alternatives, such as the soybean, are eagerly sought (Anderson 1949; Dhugga et al. 2004; Lackey 2010). Prior to my studies, the parallel presence and absence of cotyledon areoles and endosperm in papilionoid legumes has not been reported, so any functional relationship of the two has not been explored.

Nadelmann's (1890) physiological and anatomical study of legume endosperm mucilage covered 74 legume species. He concluded that the primary function of mucilage in the middle layer was a reserve carbohydrate, which is broken down during germination and moves to the cotyledons and becomes transitory starch. He speculated that the endosperm may have other functions, such as a reservoir for water or other materials. He found a complicated correlation between the degree of development of endosperm mucilage, cotyledon storage carbohydrates, and cotyledon proteins and oils, in which the increase in material in one group was associated with decreases in the others. Although he performed several microchemical tests on the

mucilage, and indicated that it is carbohydrate and is transformed into cotyledon starch during germination, he did not indicate its composition, which is now known to consist of mannose and galactose in the form of galactomannan. Avetta (1874) had previously demonstrated laboratory degradation of galactomannan into sugars. Mitchell (1930) indicates authors after Nadelmann (1890) and before 1900 with knowledge of the composition of galactomannan or "Mannogalaktan."

Pammel's (1899) study was primarily anatomical, but he did review current physiological literature, and concluded that mucilage is the reserve energy source in legumes because it is the most condensed form compared to starch, proteins, or fats. He also noted the hydrophilic nature of mucilage in endosperm in his summary of contemporary thought: "When once the water passes the Malpighian cells and reaches the endosperm the latter has a great affinity for it and additional amounts are taken up readily. . . . After the endosperm has taken up water the aleurone layer secretes a ferment which dissolves the cell-walls, and the soluble material is conveyed to the embryo."

Reid and Bewley (1979) observed in *Trigonella foenum-graecum* that removal of the endosperm seven hours after hydration still allowed germination of the embryo, although with decreased gain in weight. Because galactomannan breakdown and mobilization does not occur until much later, this observation demonstrated that any possible energy function of the endosperm galactomannan is not necessary for germination, and that galactomannan does not differ qualitatively from energy reserves in the cotyledons. Because the endosperm was never removed prior to seven hours, any necessity for galactomannan during this early period remains unknown. They confirmed the extreme hydrophilic nature of galactomannan and its role in buffering the embryo against moisture loss.

Buckeridge et al. (2000) summarized galactomannan literature and intense current interest. Galactomannans consist of a linear backbone of mannose residues with side branches of galactose residues. Galactomannans with few side branches (more or less pure mannans) are hard and insoluble in water. As branching increases, galactomannans are softer and more readily extracted with water, particularly hot water. The Caesalpinioideae tend to have abundant endosperm with galactomannans bearing few side branches. There is a trend within the Caesalpinioideae, and from Caesalpinioideae to Papilionoideae or to Mimosoideae to decreased galactomannan yields and increased branching. Galactomannans are formed within the middle endosperm cells in the Golgi (Dhugga et al. 2004) and then deposited by vesicles into the secondary cell walls. In some plants, a decrease in branching, and therefore increased hardness or density, occurs in the cell wall layer towards the lumen. Although mobilization of galactomannan during germination has been intensively studied in only a few legumes, it seems to be initiated after radicle protrusion by three enzymes of the aleurone layer, which hydrolyze galactomannan to mannose and galactose. In some legumes, hydrolytic enzymes are also stored in protein bodies within the endosperm, in addition to the aleurone layer (Tonini et al. 2010). Mannose and galactose are converted to sucrose in the endosperm, and it is transported to the cotyledons, where it forms transient starch. Recent research activity (Reid et al. 2003; Edwards et al. 2004; Dhugga 2003, 2005; Dhugga et al. 2004) demonstrates that legumes can be genetically transformed to alter galactomannan formation.

In the context of the above integrated literature summary, current observations combined with recent literature and a review of unusual galactomannan properties employed for commercial purposes suggest new functional explanations for the plant as well as variations on the three traditional functional explanations: energy reserves, water relations, and hardness for protection (Nadelmann 1890; Buckeridge et al. 2000).

Furnish energy reserves for germination

Galactomannans are known to provide energy to the germinating seed. Pammel (1899) concurs with previous workers who advocated primarily a superior energy function for galactomannan, and concluded: ". . . the plant stores away its food in the most condensed form to save space." However, current energy calculations do not support Pammel's assertion. Galactomannan has about the same energy per gram as other carbohydrates and protein, and less than half the energy per gram of oil (Lopes & Larkins 1993). As a source of energy, Reid and Bewley (1979) showed that galactomannan has no obvious advantage over other energy storage products in the cotyledons, such as oil, protein, or starch. Therefore, if galactomannan is a superior

energy storage medium, it is because of other attributes, and not because of high energy concentration or a qualitative energy superiority.

Modifies water relations during germination

Galactomannans are known to absorb and retain water (Buckeridge et al. 2000; Reid & Bewley 1979), and this is corroborated by current results. This buffering may provide a survival function for the plant. For instance, Baker and Minor (1987) found a higher frequency of visible endosperm in soybean varieties classified as weathering resistant, compared to non-weathering resistant. One can only speculate on the mechanism of selective advantage of a stable wet environment for the other seed components.

Creates hard structures to protect seed

Galactomannans are known to be hard, if few galactose side branches are present, as in many Caesalpinioideae and a few Papilionoideae (Buckeridge et al. 2000). This may serve to protect the seeds from physical harm. However, examined specimens, other than *Cyamopsis tetragonoloba*, had endosperm galactomannan softer than the external Malpighian layer. Therefore, in most specimens seen here, any protective function from galactomannan hardness is likely to be minor, and supplemental rather than primary.

Other properties

Galactomannans are known to be non-nutritional or antinutritional to many animals, including domestic birds and swine (Hsiao et al. 2006). These properties may confer chemical defense against predators. Monogastric mammals cannot break down galactomannans, and therefore they are non-nutritional molecules for a range of potential mammal seed predators. For example in human nutrition, which is monogastric, Duke (1981) gives not a single species of legume seed, normally eaten by humans, that has a conspicuous galactomannan-containing endosperm listed in Kirkbride et al. (2003). In mammals and birds, galactomannans may be also antinutritional through a number of detrimental physiological actions (Hsiao et al. 2006). In insects, Janzen (1977) studied larvae of southern cowpea weevil, a bruchid beetle, burrowing into legume seeds. Uniform tunnel size indicated that the larvae cannot break down the endosperm galactomannan and use it as a nutritional source, and therefore are more likely to starve before reaching the seed embryo.

Hydrated galactomannans are known to have several unusual commercial properties (Buckeridge et al. 2000) that may have analogous function to the seed. Galactomannans swell greatly during hydration, which cracks the testa, but the galactomannan gel remains turgid in these cracks (Fig. 2c). Galactomannan is known to form non-Newtonian fluids, that is, fluids that increase viscosity under stress. This property is widely used and researched in the petroleum extraction industry, where vast quantities of legume galactomannans are introduced under pressure into rock cracks to expand them and facilitate oil flow. Perhaps the testa cracking function in these seeds mimics the commercial use. As noted in current observations, galactomannans have adhesive, coating, and lubrication properties, which are used in the paper industry (Buckeridge et al. 2000), as well as properties that minimize ice crystal formation. Current observations suggest that lubrication and adhesion may be useful in testa shedding and retention during germination. Any utility of supression of ice formation to the seed is unknown.

Whatever the function or functions of endosperm galactomannan, it is clear that galactomannan is not a requirement for evolutionary success in papilionoid legumes. Several large and highly successful groups, such as tribe Phaseoleae subtribe Phaseolinae Bronn, including the large genera *Phaseolus* and *Vigna* lack any conspicuous endosperm, and rely on other seed energy storage molecules, and fulfill any other galactomannan functions by other means.

Cotyledon areole function

Four possible functions of the cotyledon areole have been proposed: 1) to serve as an invasion site for rhizobial bacteria, 2) to transport materials during seed development, 3) to align seed coat and embryo, and 4) to participate in germination.

Miksche (1961) proposed that the cotyledon areole serves as an invasion site for bacterial, presumably rhizobial bacterial, invasion. As Ma et al. (2004) pointed out, this is unlikely because, as corroborated in current observations, the periclinal outer walls and cutin in the cotyledon areole area are thicker than the

surrounding cotyledon epidermis, and thus less likely to be susceptible to bacterial invasion. Also, there are no literature reports of bacterial invasion in the cotyledon areole area. Additionally, now that cotyledon areole presence is known to occur widely outside of soybean, there seems no reason to suspect a correlation between cotyledon areole presence and invasion by rhizobial bacteria.

Yaklich et al. (1996) suggested that the cotyledon areole may be involved with nutrient transport and unloading to the developing embryo. For several reasons this is not likely. The cotyledon areole is initiated late in seed development, reaching full expression in the mature dormant seed, then degenerating within some days after germination (Endo & Ohashi 1999b; Ma et al. 2004). Cotyledon areole development, therefore, is not concurrent with the developing embryo. Also, the thick cuticle of the cotyledon areole would seem to impede nutrient transport, rather than facilitate it. And the peculiar presence of chloroplasts with pigments different from other cotyledon cells and protein bodies in mature endosperm does not suggest a transport function during embryo development.

Yaklich et al. (1996) and Ma et al. (2004) suggested that the cotyledon areole may help align the endosperm and embryo or maintain a round seed shape. This is also unlikely. With or without a cotyledon areole, papilionoid embryos observed here remain consistently positioned within the endosperm envelope and testa. The radicle pocket alone seems to ensure proper alignment. And in many species, cotyledon areoles are not in a depression (Endo & Ohashi 1998b; current results), which is contrary to this suggestion. Current observations suggest that presence or absence of a depression seems to bear no relation to seed shape or embryo alignment.

Yaklich et al. (1987) and Ma et al. (2004) suggested that the cotyledon areole functions in germination, possibly for transport of nutrients to the cotyledons. Although not demonstrated, this is consistent with most anatomy and known physiology. As shown in the current study, cotyledon areole and endosperm presence or absence and position are almost always positively associated, which immediately suggests a functional relationship. The position of the cotyledon areole along the midvein, or when the cotyledon areole is branched, additionally along major branch veins, suggests a transport function, as do the modified mesophyll cells between the cotyledon areole epidermis cells and the veins. It should be remembered that the veins in the mature dormant seed are not fully functional and only acquire functionality some days after imbibition, as seen in soybean (Miksche 1961), about the same time as galactomannan mobilization. The developmental and degeneration timing of cotyledon areoles corresponds with the fully mature development of endosperm and its degeneration, and the functional development of cotyledon vascular tissue. In conflict with an explanation of a germination function, the thick cuticle over the cotyledon areole would suggest a barrier to, not an enabler of transport, and the functional significance of distinctive chloroplasts, pigmentation, and protein bodies in the cotyledon areole is an enigma. It is also possible that the cotyledon areole functions in a different, and unknown, fashion during germination, such as a trigger, or as part of Varner et al.'s (1963) unknown embryo axis factor, which was a requirement for proper cotyledon metabolism.

CONCLUSIONS

At this time, the reasons why most legumes have maintained, for tens of millions of years, galactomannan bearing endosperm in the mature dormant seed is only a matter of speculation. Whatever the reason, it must have substantial selective advantage for the plants, because the deposition of the material during seed development and mobilization during germination are both precise and complicated systems involving highly specific physical, chemical, and temporal activities. Similarly, the function of the cotyledon areole is still speculative, but as shown here, the positive correlation of presence or absence, size, position, and developmental timing with endosperm suggests a functional relationship with endosperm energy reserves and germination.

Any legume seed structure, such as a cotyledon areole, must be viewed as but one component of a whole functioning seed, which has many structural, physiological, and ecological requirements for dormancy, germination, protection from predators, etc. Smith (1983) has shown through extensive survey that legume seeds occur in two basic forms. About 60% (his form 1) have endospermic seeds with foliaceous

cotyledons and epigeal germination. About 30% (his form 4) have non-endospermic seeds with enlarged storage cotyledons and usually hypogeal germination. The remainder (forms 3 and 4) have intermediate and anomalous forms. Evolution from the presumed primitive form 1 to the derived forms has occurred many times. The cotyledon areole would thus be a characteristic of form 1 seeds. How the cotyledon areole fits into the functioning of this basic form 1 is, again, unknown.

It would be instructive to study further the functional role of cotyledon areoles for several reasons. One is a general interest in seed physiology and ecology, with a possible role in legume germination strategies. A comparison with the non-cotyledon areole and scarcely studied caesalpinioid and mimosoid legume seeds could help one understand how these plants fulfill the functions of a cotyledon areole in papilionoid legumes. A second interest would be to understand the reasons for development of a very elaborate system of galactomannan accumulation and mobilization during the evolution of legumes in the early Eocene, a period much hotter and more humid than now. And third, germination of agricultural legumes, such as soybean, peas, and many others, is always a critical stage of the life cycle, and any role that the cotyledon areole may have has implications of commercial importance. The soybean would seem to be an ideal candidate for a comparative study of cotyledon areole function because the plant is well-studied, abundant material is readily available, and the diversity of wild, semiwild, and cultivated plants presents a wide range of cotyledon areole and endosperm extent from large to almost non-existent, although neither has been completely eliminated through non-scientific or scientific plant breeding.

The demonstrated correlation of cotyledon areoles with endosperm indicates that use of cotyledon areoles in systematic studies cannot be analyzed as an independent character, but must be viewed in relation to other seed and germination structures and functions, especially the endosperm.

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MICROMORFOLOGÍA DE LA LEMMA DE LOS GÉNEROS *POLYPOGON*, ×*AGROPOGON* Y *AGROSTIS* (POACEAE) EN CHILE

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RESUMEN

Las características micromorfológicas de la epidermis abaxial de la lemma de las especies que crecen en Chile de *Polypogon* Desf. (incl. *Chaetotropis* Kunth), *Agrostis* L. y ×*Agropogon* P. Fourn. (Poaceae, Pooideae, Agrostidinae) fueron estudiadas mediante microscopía electrónica de barrido (MEB). El objetivo de este trabajo es aportar nuevos caracteres que contribuyan a esclarecer la posición sistemática de algunas especies en estos géneros. Se estudiaron 24 taxones, pertenecientes a *Polypogon* (9 spp.), *Agrostis* (14 spp.) y el híbrido ×*Agropogon* (1 sp). Se analizaron 11 caracteres (7 micromorfológicos, 4 macromorfológicos) mediantes análisis de agrupamientos y de coordenadas principales. Los caracteres analizados permitieron reconocer dos grupos de especies dentro de *Polypogon*, los que se corresponden con las secciones reconocidas por Müller en 1985: *Polypogon* y *Polypogonagrostis* Asch. & Graebn. Esta última reúne las especies tratadas por otros autores bajo el género *Chaetotropis*.

ABSTRACT

The micromorphological features of the abaxial epidermis of the lemma of Chilean species of *Polypogon* Desf. (incl. *Chaetotropis* Kunth), *Agrostis* L. and the hybrid ×*Agropogon* P. Fourn. (Poaceae, Pooideae, Agrostidinae) were studied using scanning electron microscopy (SEM). The objective was to bring new characters to clarify the systematic position of some species in these genera. Twenty-four taxa belonging to *Polypogon* (9 spp.) *Agrostis* (14 spp.) ×*Agropogon* (1 sp.) were studied. Eleven characters (seven micromorphological, four macromorphological) were analyzed by cluster analysis and principal coordinates analysis. The results allowed us to recognize two groups of species within *Polypogon*, which correspond to sections recognized by Müller in 1985: *Polypogon* and *Polypogonagrostis* Asch. & Graebn. The latter comprises the species treated by other authors under the genus *Chaetotropis*.

El género *Polypogon* fue descrito por Desfontaines (1798). Pertenece a la familia Poaceae, subfamilia Pooideae, tribu Poeae, subtribu Agrostidinae (Soreng et al. 2003). El nombre del género alude a la morfología de la inflorescencia, una panícula densa provista de muchas aristas (del gr. *polys* = muchos; *pogon* = barba) (Watson & Dallwitz 1992). Las especies de *Polypogon* son conocidas por sus nombres comunes de "cola de zorro o cola de conejo," los que aluden también a la morfología de la inflorescencia.

Polypogon incluye unas 26 especies (Tzvelev 1983; Renvoize 1998; Lu & Phillips 2006) de zonas templadas y templado-cálidas de ambos hemisferios y en zonas tropicales en áreas montañosas por sobre los 1.200 m de altitud (Giraldo-Cañas 2004; Lu & Phillips 2006). Para América, Soreng et al. (2003) reconocen 11 especies, de las cuales 10 están presentes en Chile. El híbrido ×*Agropogon lutosus* (Poir.) P. Fourn. (*Agrostis stolonifera* L. × *Polypogon monspeliensis* (L.) Desf.) fue también citado para el sur Chile (Osorno, Chiloé) por Rúgolo de Agrasar & Molina (1997). Comprende plantas anuales o perennes que habitan sectores húmedos y muchas veces arenosos o salobres, en las márgenes de cursos de agua (Glenn 1987). Se caracteriza por sus espiguillas unifloras que se desprenden a la madurez con una parte o todo el pedicelo, y carecen de extensión de la raquilla; las glumas son más largas que el antecio, escabrosas y usualmente aristadas; la lemma es hialina, con 5-nervios y puede ser aristada o mútica; la pálea puede ser tan larga como la lemma o menor que ésta, alcanzando aproximadamente la mitad de su longitud (Tzvelev 1983; Nicora & Rúgolo de Agrasar 1987).

Polypogon presenta una estrecha afinidad con *Chaetotropis* (Kunth, 1829) del cual se diferencia por tener

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la pálea de una longitud menor que la mitad del largo de la lemma (Nicora & Rúgolo de Agrasar 1987). El género *Chaetotropis* ha sido aceptado, entre otros autores, por Kunth (1835), Desvaux (1854), Pilger (1920), Skottsberg (1920), Björkman (1960), Nicora (1970, 1978, 1993), Marticorena & Quezada (1985), Nicora & Rúgolo de Agrasar (1987) y Morrone et al. (2005). Otros autores, en cambio, consideran a *Chaetotropis* un sinónimo de *Polypogon*, como Kunth (1816), Trinius (1840), Steudel (1854), Martius & Eichler (1893), Stuckert (1904), Hitchcock (1931, 1951), Macbride (1936), Rosengurtt et al. (1970), Navas (1973), Gould (1983), Tzvelev (1983), Müller (1985), Clayton & Renvoize (1986), Tovar (1993), Renvoize (1998), Barkworth (2007), Zuloaga et al. (2008), Finot et al. (2009).

El tratamiento taxonómico más completo de las especies de *Polypogon* s.l. fue realizado por Müller (1985) quien reconoce 10 especies reunidas en dos secciones: *Polypogon* sect. *Polypogon* tipificada por *P. monspeliensis*, con seis especies y *Polypogon* sect. *Polypogonagrostis* Asch. & Graeb. tipificada por *P. elongatus*, con cuatro especies. Müller (1985) caracteriza la sección *Polypogonagrostis* como plantas perennes, con glumas aristadas desde el ápice, con lemmas de ca. 1.5 mm de largo, pálea más corta que la lemma que alcanza hasta 2/5–1/3 de su largo y epidermis de la lemma provista de una malla de engrosamientos de la pared periclinal de las células epidérmicas denominada "trichodium net" (Rúgolo de Agrasar & Molina 1997a; Favret et al. 2007).

En la sección *Polypogonagrostis*, Müller (1985) incluye a *P. chilensis* (Kunth) Pilger (= *Ch. chilensis* Kunth), *P. elongatus* Kunth (= *Ch. elongata* (Kunth) Björkman), *P. rioplatensis* Herter (= *Ch. rioplatensis* (Herter) Björkman) y *P. imberbis* (Phil.) Johow (= *Ch. imberbis* (Phil) Björkman). De éstas, *P. rioplatensis* se considera actualmente un sinónimo de *P. imberbis* (Soreng et al. 2003).

La sección *Polypogon* fue caracterizada por Müller (1985) como aquella que comprende plantas anuales o perennes, con glumas aristadas desde el ápice o con el ápice bilobado, aristado desde la incisión de los dos lóbulos en que se divide el ápice, lemma de hasta 1,5 mm de largo, sin *trichodium net* y la pálea tan larga como la lemma o poco menor que ésta. En esta sección incluye a *P. australis* Brongn., *P. interruptus* Kunth, *P. linearis* Trin., *P. maritimus* Willd., *P. monspeliensis* (L.) Desf. y *P. viridis* (Gouan) Breistr. Con la excepción de *P. rioplatensis*, todas las restantes especies tratadas por Müller (1985) han sido citadas para Chile (Marticorena & Quezada 1985; Soreng et al. 2003; Zuloaga et al. 2008). A estas especies hay que agregar *P. exasperatus* (Trin.) Renvoize (= *Agrostis exasperata* Trin.) y *P. hackelii* (R.E. Fr.) Renvoize (= *Ch. hackelii* (R.E. Fr.) Björkman) transferidas a *Polypogon* desde el género *Agrostis* por Renvoize (1998). Ambas especies debieran incluirse en la sección *Polypogonagrostis* por poseer la pálea más corta que la lemma.

La presencia de la malla de engrosamientos en la epidermis de la lemma ha sido considerada un carácter útil para distinguir las secciones *Polypogon* y *Polypogonagrostis,* o bien para distinguir el género *Chaetotropis* de *Polypogon*. No obstante, especies de otros géneros como *Agrostis* L., *Deyeuxia* Clarion ex P. Beauv. (*D. parviseta* Vickery) y *Bromidium* Nees & Meyen (*B. hygrometricum* (Nees) Nees & Meyen, *B. ramboi* (Parodi) Rúgolo), también presentan malla (Favret et al. 2007), así como dentro de *Agrostis* carecen de malla las especies del subgénero *Zinagrostis* Romero-García, Blanca & Morales-Torres (*A. truncatula* Parl., *A. reuteri* Boiss. y *A. nebulosa* Boiss. & Reuter), lo que hace que el valor taxonómico de la malla sea discutible.

Polypogon también presenta una estrecha afinidad con *Agrostis* descrito por Linnaeus (1753). Estos géneros se distinguen porque en *Agrostis* las espiguillas se desarticulan sobre las glumas quedando éstas persistentes en la inflorescencia a la madurez de los frutos luego del desprendimiento del antecio; en *Polypogon*, en cambio, las espiguillas se desarticulan con todo o parte del pedicelo, de modo que las glumas caen junto con el antecio que queda unido al resto de la espiguilla a la madurez de los frutos (Rúgolo de Agrasar 1982; Clayton & Renvoize 1986).

El híbrido ×*Agropogon* muestra caracteres intermedios entre *Agrostis* y *Polypogon*. En este género el antecio se desarticula y se desprende de las glumas como ocurre en *Agrostis*, pero las glumas aristadas y escabrosas, que se desprenden con el pedicelo, recuerdan a *Polypogon* (Rúgolo de Agrasar & Molina 1997b).

Los objetivos del presente trabajo fueron examinar y describir la epidermis abaxial de la lemma de las especies estudiadas mediante microscopía electrónica de barrido (MEB), comparar las especies sobre la base de los caracteres micro y macro morfológicos de la lemma y discutir la posición sistemática de algunas especies en los géneros *Polypogon*, *Agrostis* y ×*Agropogon*.

TABLA 1. Caracteres y estados de carácter utilizados en los análisis multivariados.

Carácter	**Abreviatura**	**Estados**
Malla	M	0 = ausente 1 = presente, poco desarrollado 2 = presente, bien desarrollado
Aguijones	AG	0 = ausentes 1 = 1-5 aguijones/campo 2 = 6-15 aguijones/campo 3 = ≥ 16 aguijones/campo
Ondulación de la pared anclinal de las células largas	ON	0 = recta 1 = recta y ondulada 2 = ondulada
Engrosamiento de la pared anclinal de las células largas	EN	0 = ausente 1 = presente
Ancho de las células epidérmicas	AC	µm
Tipo de engrosamiento de la malla	TEM	0 = laxo, distancia entre engrosamientos igual o mayor que los engrosamientos 1 = compacto, distancia entre engrosamientos menor que los engrosamientos
Forma de los engrosamientos de la malla	FEM	0 = elíptico 1 = subrectangular 2 = irregular
Pelos del callus	PC	0 = ausentes 1 = cortos, menores que el largo de la lemma 2 = largos, mayores que el largo de la lemma
Arista	AR	0 = ausente 1 = presente 2 = ausente o presente
Desprendimiento de la espiguilla	DE	0 = desprendimiento sobre la gluma 1 = desprendimiento bajo la gluma
Relación de la longitud de la pálea respecto a la lemma	RLPL	0 = pálea (1/2–2/3) de la longitud de la lemma 1 = pálea (3/4–1) de la longitud de la lemma

MATERIALES Y MÉTODOS

Para este estudio se revisaron ejemplares de los herbarios BA, CONC, SI y SGO (Holmgren et al. 1990). Los especímenes estudiados se señalan en el Anexo 1. Las lemmas se obtuvieron utilizando una pinza de punta fina y fijadas en un portamuestras de aluminio con ayuda de una cinta adhesiva de carbón conductivo. Luego fueron secadas a punto crítico (O_2 líq., 31°C, 80 atm), metalizadas con oro a 500 A° de espesor en un metalizador Edwards S-150 y observadas en un microscopio electrónico de barrido marca JEOL modelo JSM-6380LV en el laboratorio de Microscopía Electrónica de la Universidad de Concepción.

Las fotografías digitales de la epidermis fueron realizadas en la zona basal, media y apical de las lemmas, con el objeto de detectar diferencias en la disposición de las células u ornamentación a lo largo de la lemma. Las dimensiones están dadas en micrones (µm). Para la descripción de la epidermis se sigue la terminología de Ellis (1979). Los caracteres epidérmicos observados y las abreviaturas de éstos se muestran en la Tabla 1. Se construyó una matriz básica de datos (MBD) (Tabla 2) que incluyó 11 caracteres, de los cuales 7 corresponden a características micromorfológicas epidérmicas de la lemma (ancho de las células largas, presencia/ausencia de aguijones, presencia/ausencia de malla, tipo de engrosamiento de la malla, forma de

Tabla 2. Matriz básica de datos de los caracteres utilizados para el análisis multivariado. **M** = malla; **AG** = aguijones; **ON** = ondulación de la pared anticlinal de las células largas; **EN** = engrosamiento de la pared anticlinal de las células largas; **AC** = ancho de las células largas; **TEM** = tipo de engrosamiento de la malla; **FEM** = forma de los engrosamientos de la malla; **PC** = longitud de los pelos del callus; **AR** = arista; **na** = no aplicable; DE = Desprendimiento de la espiguilla; **RLPL** = Relación de la longitud de la pálea respecto a la lemma.

Especies	M	AG	ON	EN	AC	TEM	FEM	PC	AR	DE	RLPL
Polypogon* sect. *Polypogon											
P. australis	0	1	0	1	5,6	na	na	0	1	1	1
P. interruptus	0	0	0	0	4,5	na	na	0	1	1	1
P. linearis	0	0	0	0	6,2	na	na	0	1	1	1
P. monspeliensis	0	0	1	0	6,2	na	na	0	1	1	1
P. viridis	0	0	1	0	5,1	na	na	0	0	1	1
Polypogon* sect. *Polypogonagrostis											
P. chilensis	1	0	2	1	7,3	1	0	0	2	1	0
P. elongatus	1	0	2	1	5,7	1	0	0	1	1	0
P. exasperatus	1	0	2	1	5,6	1	2	1	1	1	0
P. imberbis	1	0	2	1	5,1	1	2	0	0	1	0
Agrostis											
A. brachyathera	1	3	1	1	6,8	0	0	1	1	0	0
A. breviculmis	1	2	0	1	7,3	1	1	1	0	0	0
A. glabra	1	0	2	1	6,3	1	2	1	0	0	0
A. imberbis	1	2	2	1	6,8	0	1	1	0	0	0
A. inconspicua	1	3	2	1	4,3	0	2	1	2	0	0
A. insularis	1	1	2	1	5,7	1	1	2	0	0	0
A. kuntzei	0	0	2	0	6,2	na	na	1	1	1	0
A. magellanica	0	0	2	1	5,6	na	na	1	1	1	0
A. masafuerana	1	3	2	1	5,1	1	1	1	1	0	0
A. mertensii	1	3	0	1	5,6	1	2	1	1	0	0
A. philippiana	0	1	2	0	5,6	na	na	0	0	0	0
A. scabra	1	2	2	1	6,2	1	2	1	1	0	0
A. stolonifera var. *palustris*	1	3	2	0	6,8	1	0	1	0	0	1
A. stolonifera var. *stolonifera*	1	3	2	1	6,8	1	0	1	0	0	1
xAgropogon											
A. lutosus	0	1	2	0	4,5	na	na	0	1	0	1

los engrosamientos de la malla, engrosamiento de la pared anticlinal de las células largas y ondulación de la pared anticlinal de las células largas) y 4 a características macromorfológicas (pelos del callus, presencia o ausencia de arista, desarticulación de la espiguilla y largo de la pálea en relación al largo de la lemma). La incorporación de los dos últimos caracteres responde a que han sido ampliamente utilizados para reconocer las especies del género *Chaetotropis*. La MBD fue analizada mediante análisis de conglomerados utilizando el algoritmo de Ward, que entrega grupos mutuamente exclusivos, donde cada grupo incluye los miembros con la mayor similitud otorgando la máxima homogeneidad interna (Ward 1963) y el coeficiente de distancia de Gower, que permite el uso de variables cualitativas y cuantitativas simultáneamente (Gower 1966), para la confección de un fenograma y un análisis de coordenadas principales; utilizando el programa estadístico Infostat 2009 (Di Rienzo et al. 2009).

RESULTADOS

En las especies estudiadas, la epidermis de la lemma mostró células largas (Fig. 7A–D), *malla* (Figs. 1–6) y tricomas (aguijones) (Fig. 1A–D). No se observó la presencia de estomas, células cortas ni macropelos.

La longitud de células largas pudo ser observada sólo en *Polypogon* sect. *Polypogon* (Fig. 7A–D), ×*Agropogon lutosus* (Fig. 7E–F), *Agrostis kuntzei* (Fig. 3A–B), *A. magellanica* (Fig. 3C–D) y *A. philippiana* (Fig. 4C–D), pues en las restantes especies de *Agrostis* y en *Polypogon* sect. *Polypogonagrostis* la presencia de malla impide distinguir el largo de las células. En la sección *Polypogon* las células largas miden de 60–160 µm de largo por 3–7 µm

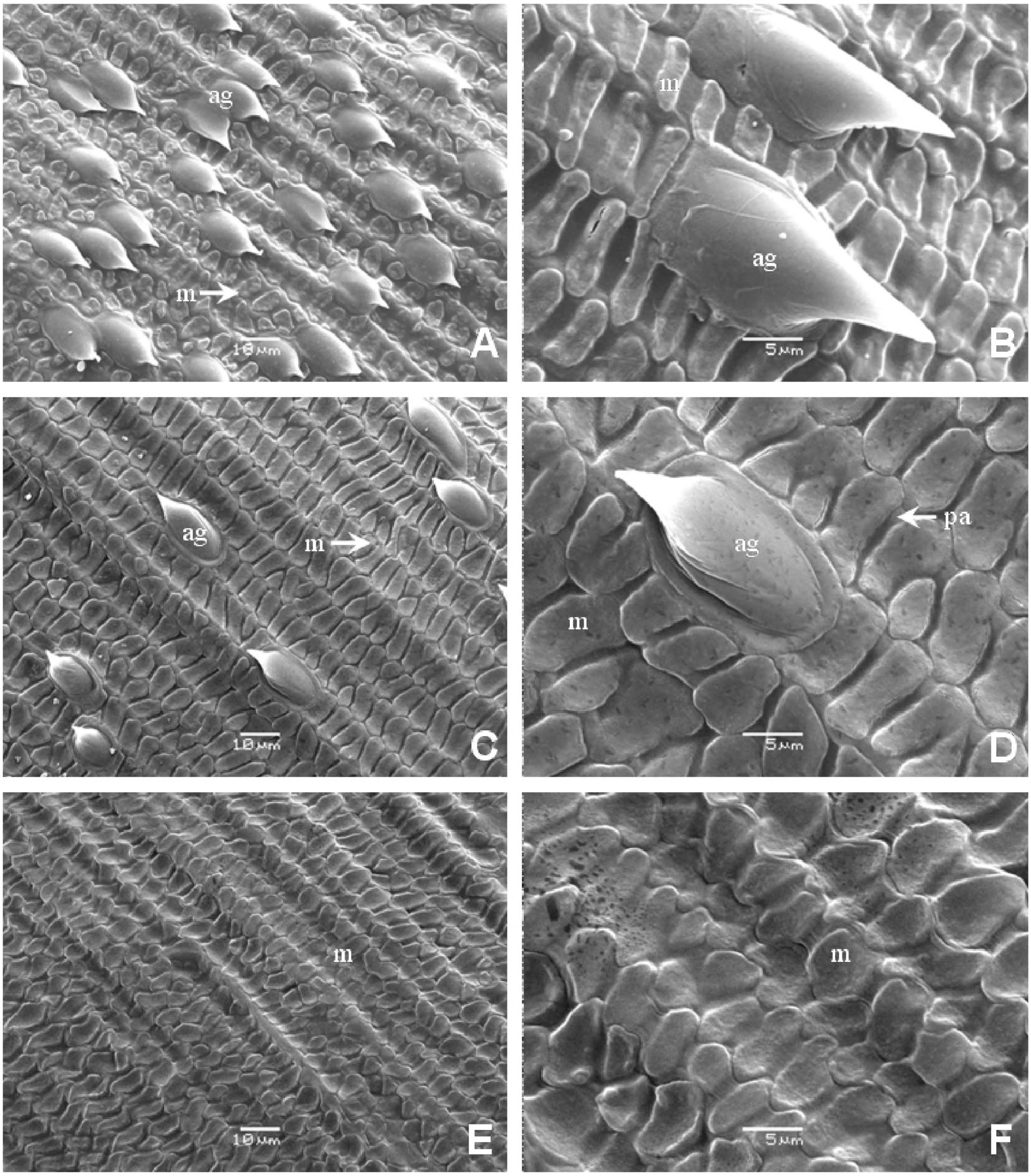

Fig. 1. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Agrostis*. A–B. *Agrostis brachyathera* A. (1000x), B. (3000x) (*Finot & López 1442,* CONC); C–D. *Agrostis breviculmis* C. (1000x) *(Mihoc et al. 4437,* CONC), D. (3000x) (*Ruiz & López 914*, CONC); E–F. *Agrostis glabra* E. (1000x), F. (3000x) *(Dominguez 160,* CONC); ag, aguijones; m, malla; pa: pared de célula larga.

de ancho. La pared anticlinal de las células largas puede ser recta, como en *Agrostis breviculmis* Hitch. (Fig. 1C–D), *A. mertensii* Trin. (Fig. 4A–B), *Polypogon australis* (Fig. 7A–B), *P. interruptus* (Tabla 2) y *P. linearis* (Fig. 7C–D) u ondulada en forma de U, como en ×*Agropogon lutosus* (Poir.) P. Fourn. (Fig. 7E–F), *Agrostis glabra* (J. Presl) Kunth (Fig. 1E–F), *A. imberbis* Phil. (Fig. 2A–B), *A. inconspicua* Kunze ex E. Desv. (Fig. 2C–D), *A. insularis* Rúgolo & Molina (Fig. 2E–F), *A. kuntzei* Mez (Fig. 3A–B), *A. magellanica* Lam. (Fig. 3C–D), *A.*

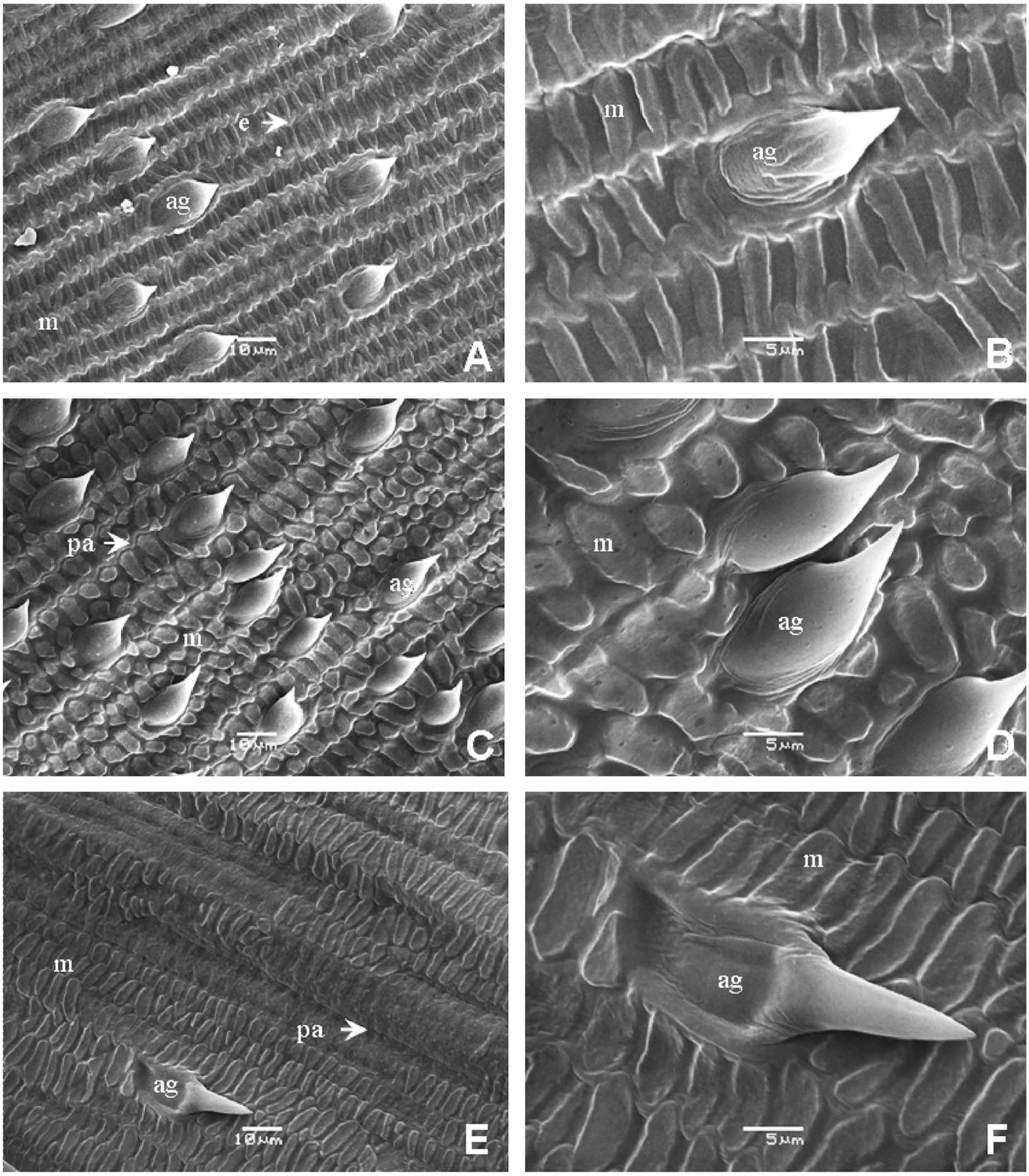

Fig. 2. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Agrostis*. A–B. *Agrostis imberbis* A. (1000x), B. (3000x) (*Marticorena* & *Matthei 898*, CONC); C–D. *Agrostis inconspicua* C. (1000x) (*Teneb 577*, CONC), D. (3000x) (*Soreng* & *Soreng 7136* CONC); E–F. *Agrostis insularis* E. (1000x), F. (3000x) (*Villagrán* & *Aguila 6063,* CONC). ag, aguijones; m, malla; e, engrosamiento de la pared anticlinal; pa, pared anticlinal.

masafuerana Pilg. (Fig. 3E–F), *A. philippiana* Rúgolo & De Paula (Fig. 4C–D), *A. scabra* Willd. (Fig. 4E–F), *A. stolonifera* L. var. *palustris* (Huds.) Farw. (Fig. 5A–B) y var. *stolonifera* (Fig. 5C–D), *P. chilensis*, *P. elongatus* (Fig. 6A–B), *P. exasperatus* (Fig. 6C–D), *P. imberbis* (Fig. 6E–F). En *A. brachyathera* Steud., *P. monspeliensis* y *P. viridis* se observaron células largas con paredes rectas y onduladas en la misma epidermis. Engrosamiento de la pared anticlinal fue observado en la mayor parte de las especies de *Agrostis* (Fig. 2A), en todas las especies de la sect. *Polypogonagrostis* (Fig. 6B) y en *P. australis* (Fig. 7A–B). Carecen de engrosamiento en la

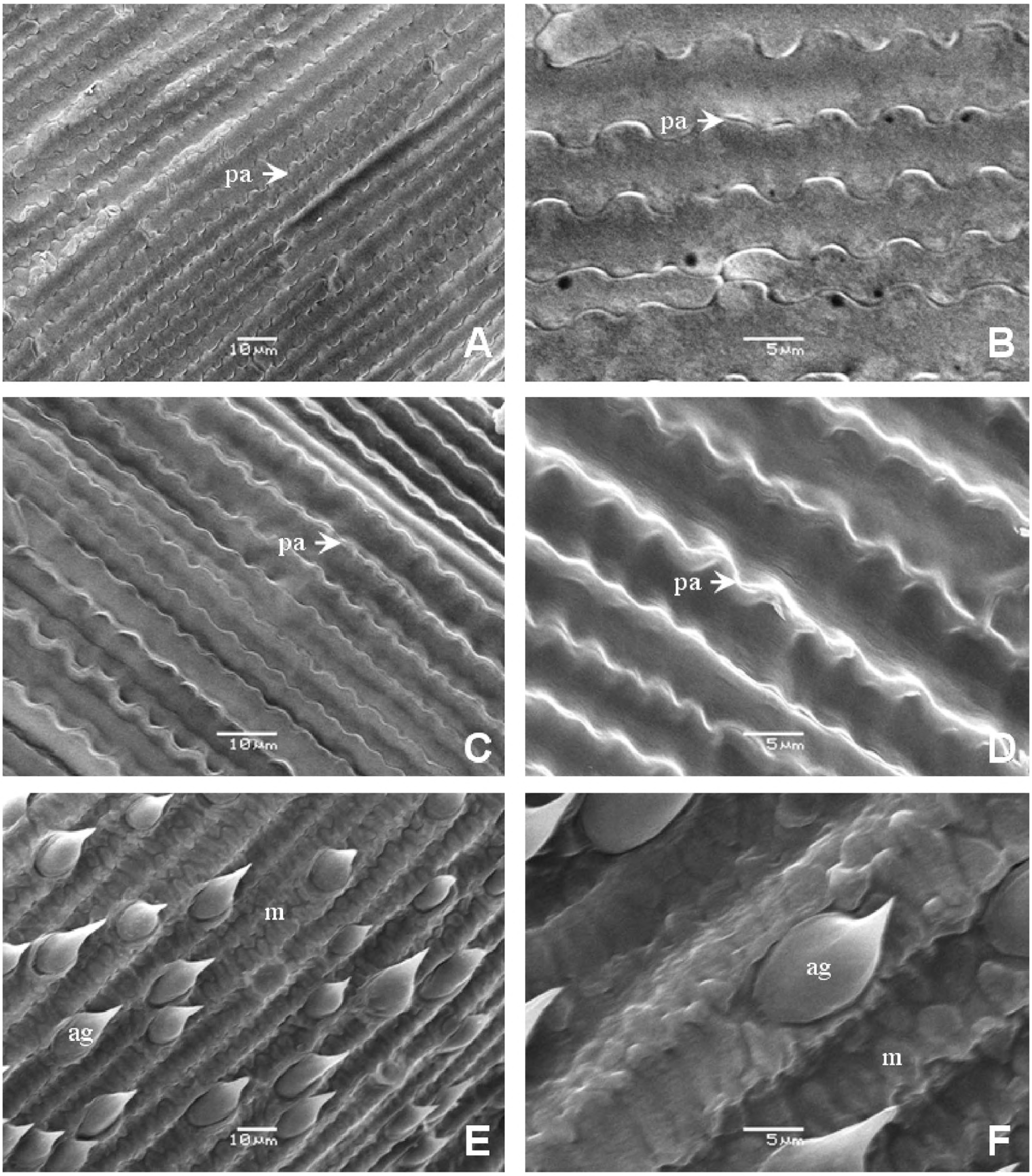

Fig. 3. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Agrostis*. A–B. *Agrostis kuntzei* A. (1000x), B. (3000x) (*Jiles 1184,* CONC); C–D. *Agrostis magellanica* C. (1000x) (*García 3958*, CONC), D. (3000x) (*Pisano 2527,* CONC); E–F. *Agrostis masafuerana* E. (1000x), F. (3000x) (*Landero* & *Gaete 9155*, CONC). ag, aguijones; m, malla; pa, pared anticlinal.

pared anticlinal *A. kuntzei* (Fig. 3A), *A. philippiana* (Fig. 4C), *A. stolonifera* var. *palustris* (Fig. 5A) y todas las especies de la sect. *Polypogon* (Fig. 7C–D) con excepción de *P. australis*.

Los aguijones presentaron una base oval y una espina apical usualmente más corta que la base (Fig. 1A–D). En *Agrostis*, los aguijones miden 10–30 µm de largo y se distribuyen homogéneamente a lo largo de la lemma; en *P. australis* disminuyen hacia el ápice. En algunas especies son muy abundantes, como en *A. brachyathera* (Fig. 1A–B), *A. inconspicua* (Fig. 2C–D), *A. masafuerana* (Fig. 3E–F), *A. mertensii* (Fig. 4A–B), *A.*

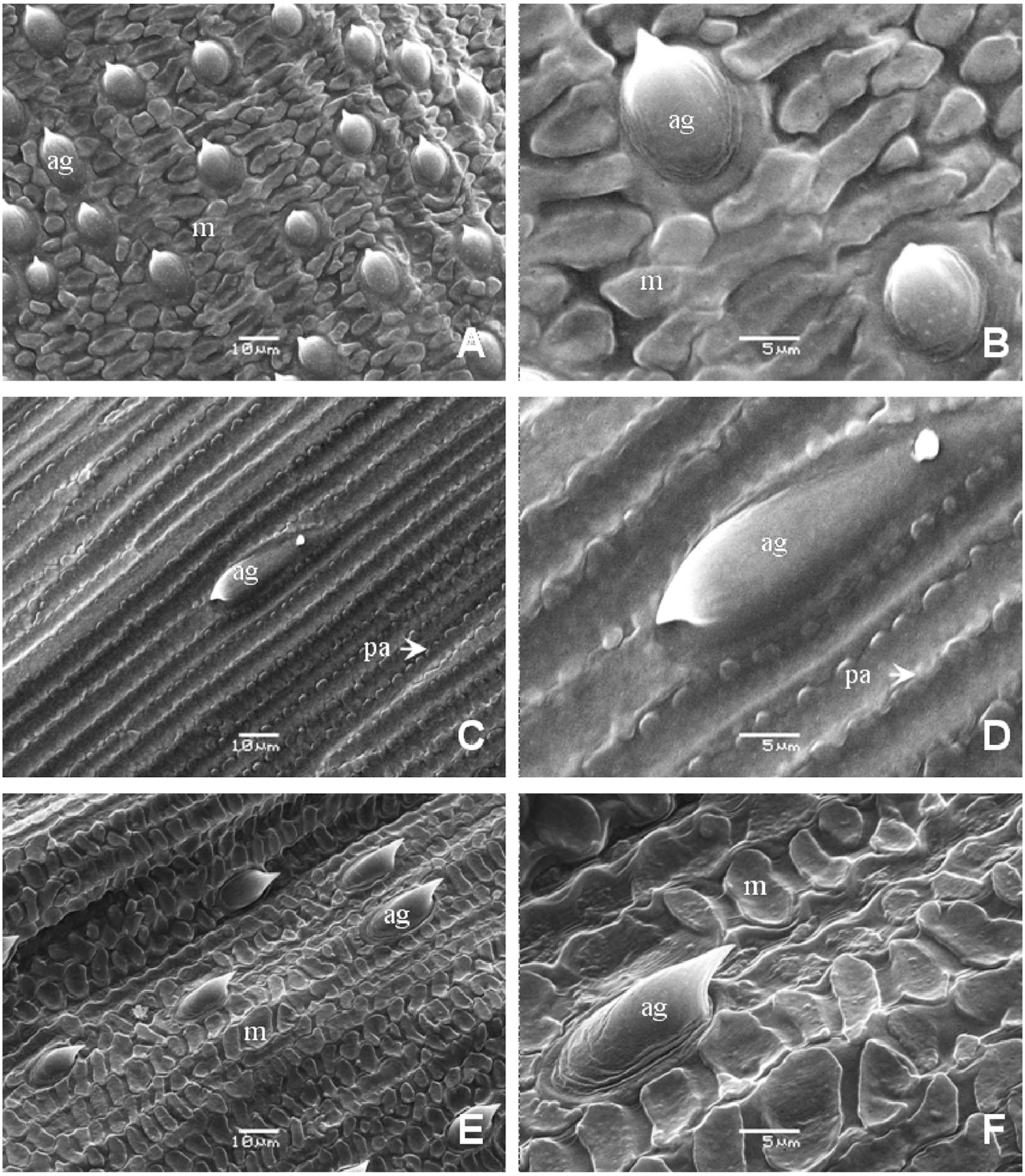

Fig. 4. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Agrostis*. A–B. *Agrostis mertensi* A. (1000x), B. (3000x) *(Finot & López 1746*, CONC); C–D. *Agrostis philippiana* C. (1000x) (*Mihoc et al. 4102*, CONC), D. (3000x) (*Baeza & Finot 3670*, CONC); E–F. *Agrostis scabra* E. (1000x), F. (3000x) (*Garcia 3948*, CONC). ag, *aguijones;* m, malla; pa, pared anticlinal.

stolonifera var. *palustris* (Fig. 5A–B) y var. *stolonifera* (Fig. 5C–D) con cerca de 16–25 aguijones por campo visual (1800 μm^2) o muy escasos, como en *Agrostis insularis* (Fig. 2E–F), *A. philippiana* (Fig. 4C–D), *P. australis* (Fig. 7A–B), ×*Agropogon lutosus* (Fig. 7E–F) con 1–5 aguijones por 1800 μm^2. Todas las especies de la sect. *Polypogonagrostis* carecen de aguijones en la epidermis de la lemma (Figs. 5E–F, 6); en la sect. *Polypogon* fueron observados sólo en *P. australis*. En cambio, la mayor parte de las especies de *Agrostis* presentaron aguijones

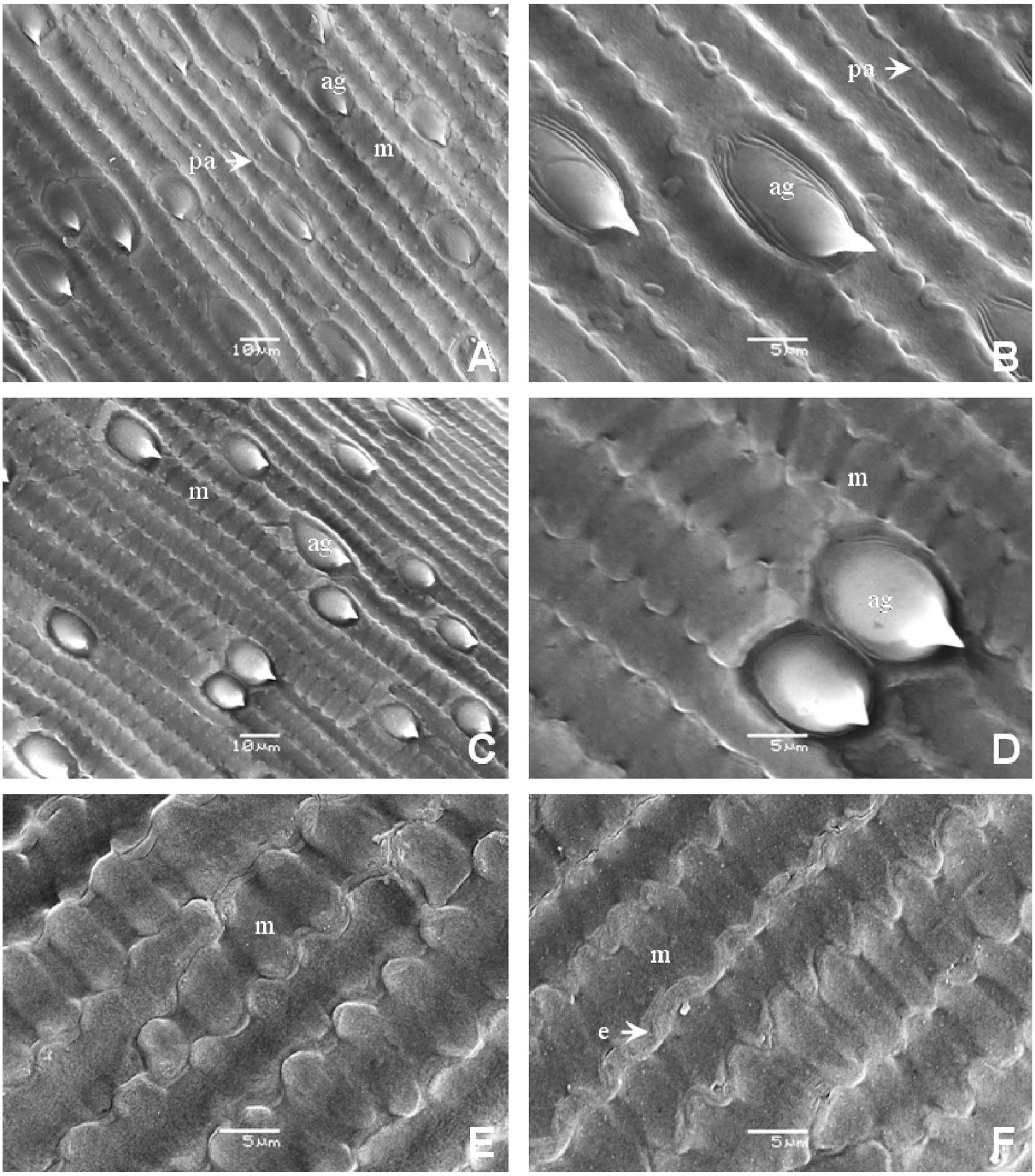

Fig. 5. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Agrostis* y *Polypogon* sect. *Polypogonagrostis*. A–B. *Agrostis stolonifera var. palustris* A. (1000x) (*Villagrán & Leiva 7557*, CONC), B. (3000x) (*Parra & Torres 669*, CONC); C–D. *Agrostis stolonifera var. stolonifera* C. (1000x), D. (3000x) (*Peterson & Soreng 15620*, CONC); E–F. *Polypogon chilensis* E (3000x) (*Villagrán 4899*, CONC), F. (3000x) *(Villagrán et al. 6954,* CONC). ag, aguijones; e, engrosamiento pared anticlinal; m, malla; pa, pared anticlinal.

epidérmicos, con la excepción de *A. glabra* (Fig. 1E–F), *A. kuntzei* (Fig. 3A–B) y *A. magellanica* (Fig. 3C–D). En todas las especies las aristas de la lemma presentaron aguijones (no mostrado).

La malla fue observada en todas las especies de *Agrostis* (excepto *A. kuntzei*, *A. magellanica* y *A. philippiana*) (Figs. 3A–D, 4C–D) así como en la sección *Polypogonagrostis*. Las especies pertenecientes a la sección *Polypogon* (Fig. 7A–D) y ×*Agropogon lutosus* (Fig. 7E–F) no presentan malla. En general, la malla se presentó

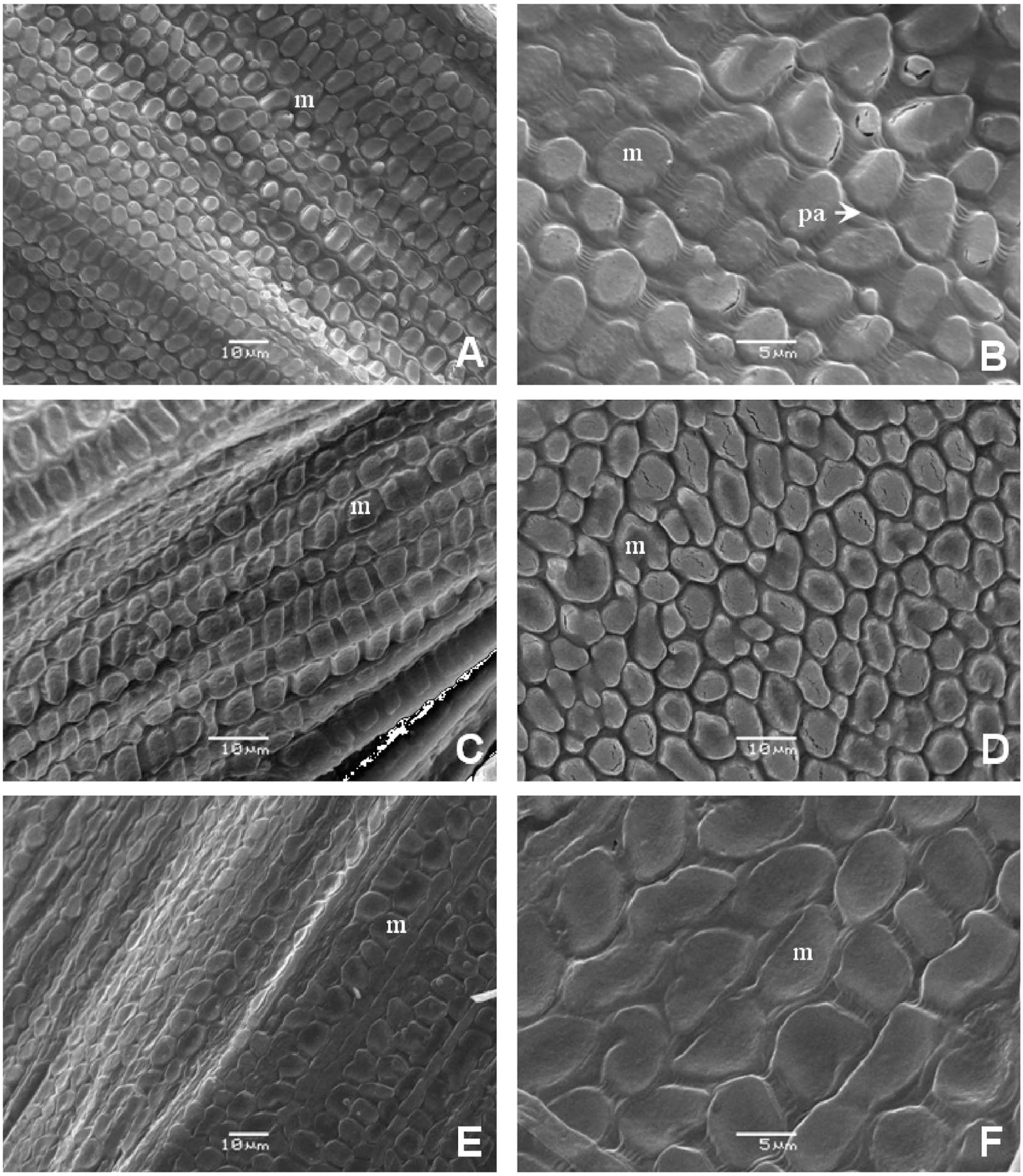

Fig. 6. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Polypogon* sect. *Polypogonagrostis*. A–B. *Polypogon elongatus*. A. (1000x), B. (3000x) (*Tedane 5221*, SI); C–D. *Polypogon exasperatus*. C. (1000x) (*Araya 69*, CONC), D. (3000x) (*Levi 1742*, CONC); E–F. *Polypogon imberbis* E. (1000x), F. (3000x) (*Villagrán* & *Leiva 7280*, CONC). ag, aguijones; m, malla; pa, pared anticlinal.

como engrosamientos de contorno elíptico (Fig. 5E–F), subrectangular (Fig. 2F) o irregular (Fig. 4F). El eje mayor del engrosamiento es siempre perpendicular al eje mayor de la lemma. La malla presentó una estructura compacta en *A. breviculmis*, *A. glabra*, *A. insularis*, *A. masafuerana*, *A. mertensii*, *A. scabra*, *A. stolonifera* y en todas las especies de la sect. *Polypogonagrostis*. Se consideró malla de tipo compacto cuando el espacio entre engrosamientos fue menor que el eje menor del engrosamiento, paralelo al eje mayor de la lemma (Fig. 1D).

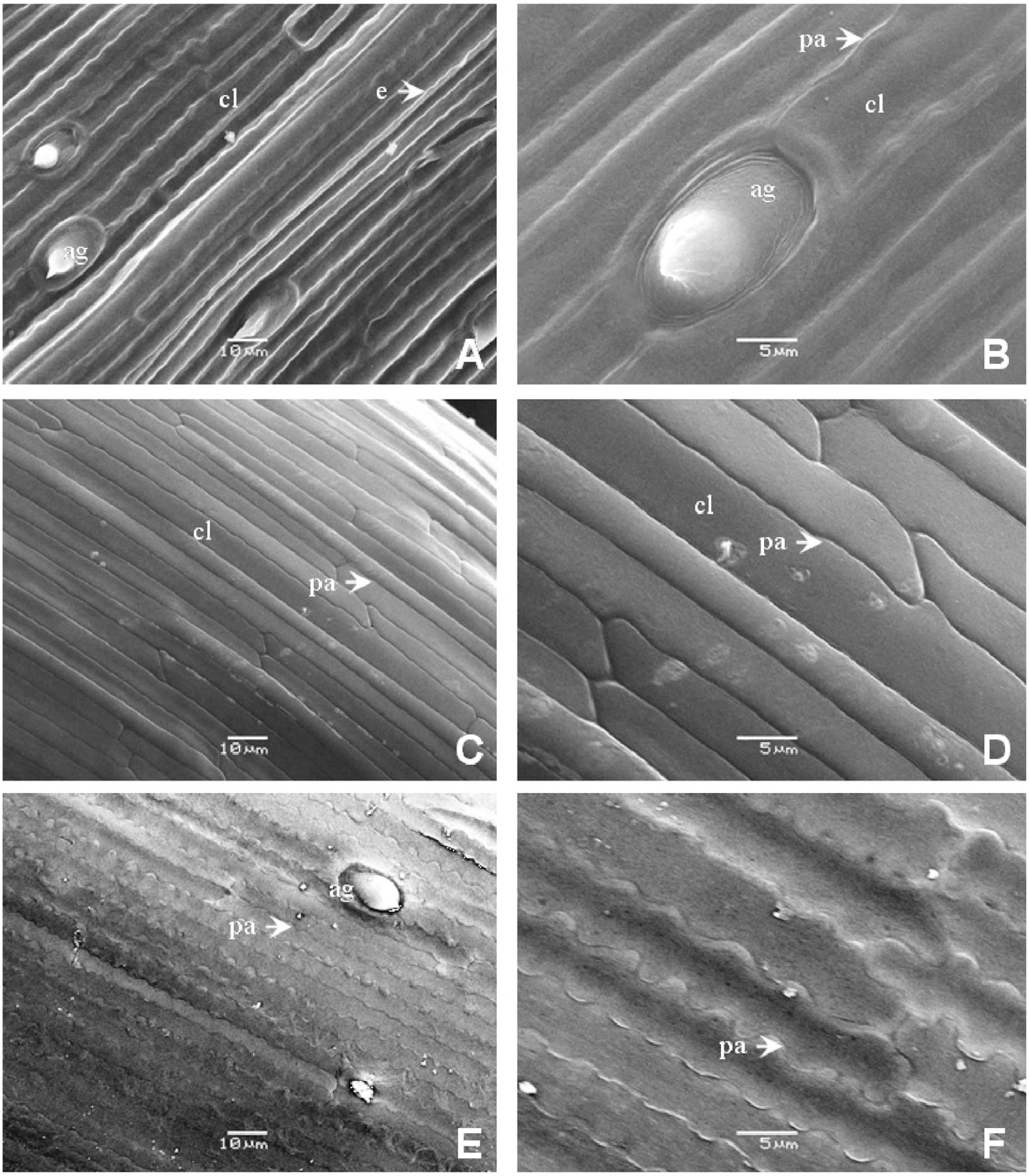

Fig. 7. Fotomicrografías de MEB de la epidermis de la lemma en especies de *Polypogon* sect. *Polypogon*. A–B. *Polypogon australis*. A. (1000x) (*Pisano & Bravo 200,* CONC), B. (3000x) (*Gardner & Knees 6974*, CONC); C–D. *Polypogon linearis*. C. (1000x), D. (3000x) (*Bliss & Lusk 808*, CONC); E–F. ×*Agropogon lutosus*. E. (1000x), F. (3000x) (*Rúgolo de Agrasar 1218*, SI). Ag, aguijones; cl, células largas; e, engrosamiento pared anticlinal; m, malla; pa, pared anticlinal.

Cuando el espacio entre engrosamientos fue mayor o igual que el eje menor del engrosamiento (Fig. 2B), la malla se definió como laxo.

En *Agrostis*, la presencia de arista en el dorso de la lemma fue observada en *A. brachyathera*, *A. kuntzei*, *A. magellanica*, *A. masafuerana*, *A. mertensi* y *A. scabra*. *Agrostis magellanica* y *A. mertensi* muestran una arista geniculada inserta en el medio del dorso de la lemma y que excede ampliamente la longitud de las glumas.

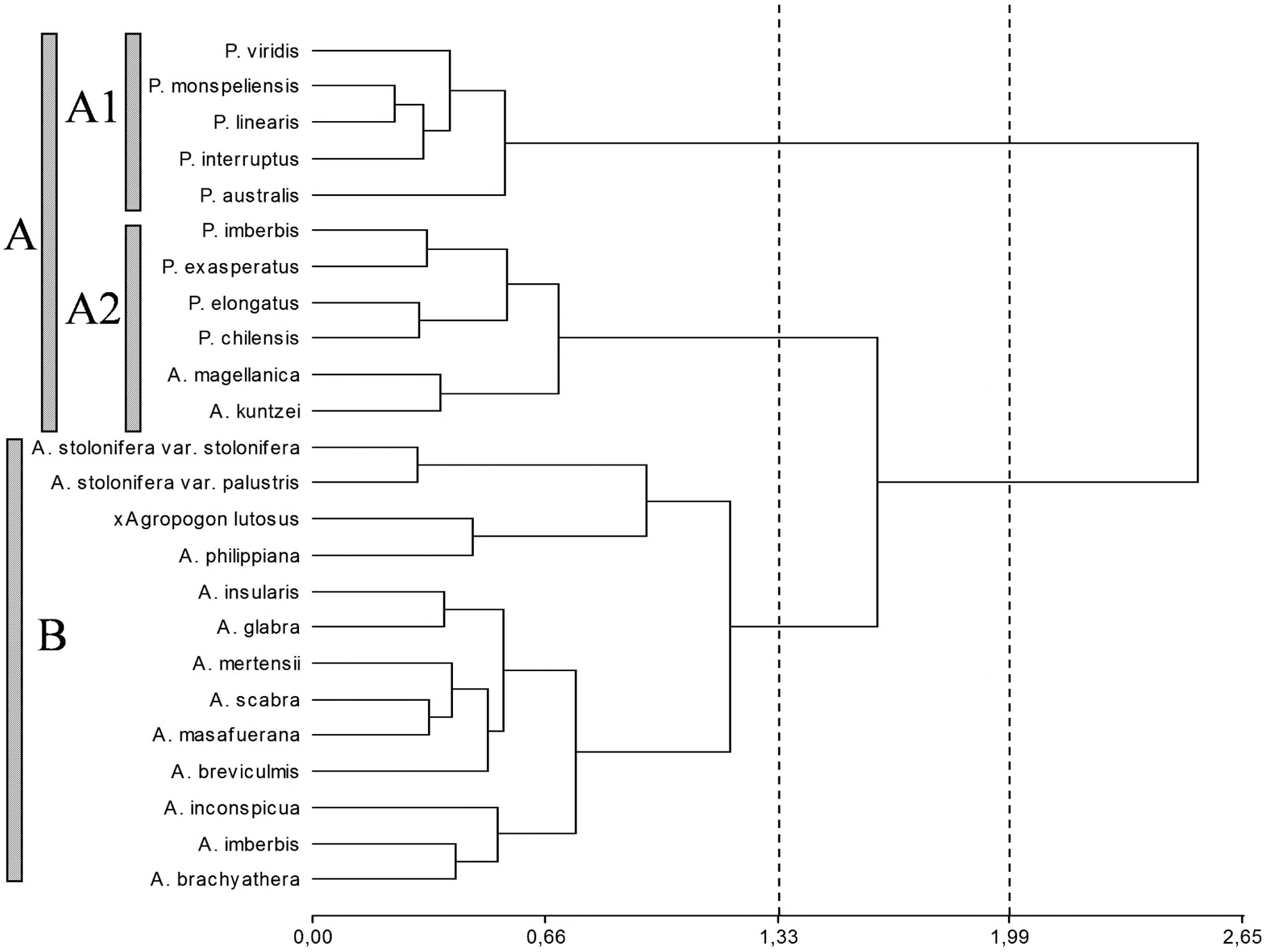

Fig. 8. Fenograma de Ward basado en una matriz de distancias de Gower utilizando 11 caracteres y 24 OTUs. Correlación cofenética = 0,735. A = *Polypogon*; A1 = *Polypogon* sect. *Polypogon*; A2 = *Polypogon* sect. *Polypogonagrostis*; B = *Agrostis* + ×*Agropogon*.

Otras especies, como *A. brachyathera*, *A. glabra* y *A. scabra* presentan una arista muy corta, que no sobrepasa el largo de las glumas. En *Agrostis inconspicua* la arista puede estar ausente o presente, pero no suele sobrepasar el largo de las glumas. En la sección *Polypogonagrostis* todas las especies presentan aristas rectas y delicadas, aunque en *P. imberbis* y *P. elongatus* es muy breve y en *P. chilensis* la arista puede estar ausente. En la sección *Polypogon*, sólo carece de arista *P. viridis*. ×*Agropogon lutosus* presentó arista geniculada más larga que las glumas.

Con la excepción de *A. insularis*, que presentó pelos del callus largos que superan el largo de la lemma, las restantes especies presentaron callus glabro (*A. philippiana*, *P. chilensis*, *P. elongatus*, *P. imberbis*, *P. australis*, *P. interruptus*, *P. linearis*, *P. monspeliensis*, *P. viridis* y ×*Agropogon lutosus*) o con pelos muy cortos y escasos (*A. brachyathera*, *A. breviculmis*, *A. glabra*, *A. imberbis* Phil., *A. inconspicua*, *A. kuntzei*, *A. magellanica*, *A. masafuerana*, *A. mertensi*, *A. scabra* y *A. stolonifera* var. *palustris*, *A. stolonifera* var. *stolonifera* y *P. exasperatus*).

La desarticulación de la raquilla coincide con la clasificación genérica, con la excepción de *A. kuntzei* y *A. magellanica* que desarticulan bajo las glumas, desprendiéndose las espiguillas con todo o parte del pedicelo, como se observó en todas las especies de *Polypogon*. En ×*Agropogon lutosus* la raquilla desarticula sobre las glumas.

La pálea está poco desarrollada en la mayor parte de las especies estudiadas. Sólo iguala a la lemma o es poco menor que ésta en *Polypogon* sect. *Polypogon*, ×*Agropogon*, *Agrostis stolonifera* var. *palustris* y var. *stolonifera*.

El fenograma (Fig. 8) muestra dos grupos que se separan a una distancia de 1.99. El primero de ellos,

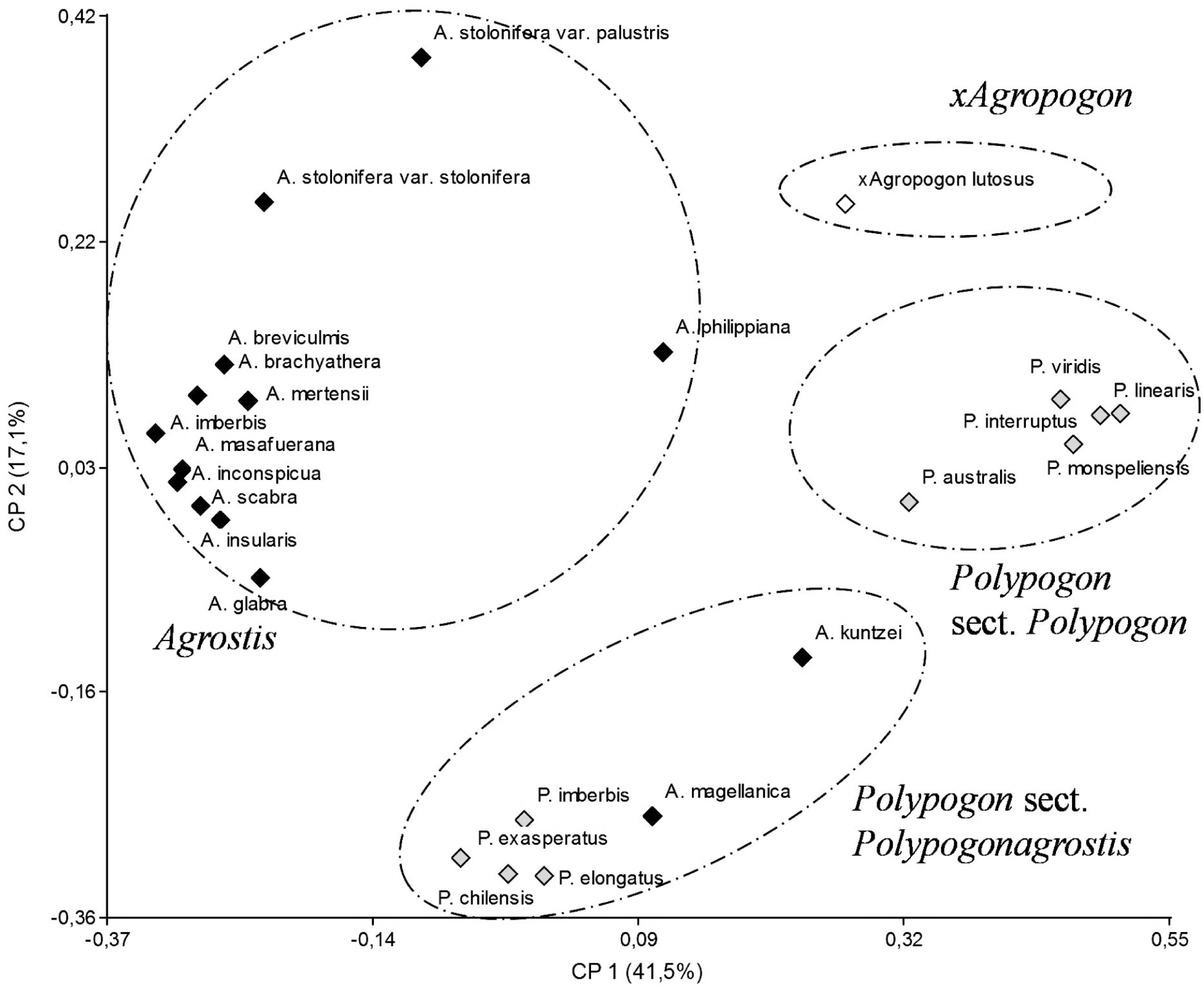

Fig. 9. Análisis de coordenadas principales de 24 OTUs y 9 caracteres de *Agrostis*, ×*Agropogon* y *Polypogon*.

A1, corresponde a *Polypogon* sect. *Polypogon*. El segundo grupo incluye a los géneros ×*Agropogon*, *Agrostis* y *Polypogon* sect. *Polypogonagrostis*. A una distancia de 1.33, se reconocen tres grupos: *Polypogon* sect. *Polypogon* (A1), *Polypogon* sect. *Polypogonagrostis* (A2) y *Agrostis* + ×*Agropogon* (B). La distribución de las especies en el fenograma coincide con la clasificación genérica excepto para *A. kuntzei* y *A. magellanica* que quedan incluidas en el grupo A2 que reúne a las especies de la sección *Polypogonagrostis*.

La distribución de las OTUs en las dos primeras coordenadas principales muestra cuatro grupos (Fig. 9), que en general coinciden con los grupos obtenidos por el análisis de conglomerados, con la excepción de ×*Agropogon lutosus* que ocupa una posición intermedia entre *Agrostis* y *Polypogon* sect. *Polypogon*. *Agrostis kuntzei* y *A. magellanica* se asocian a las especies de la sección *Polypogonagrostis*, a la vez que éstas se distinguen de *Polypogon* sect. *Polypogon* a lo largo de la primera coordenada. *Agrostis* (exceptuando *A. kuntzei* y *A. magellanica*) conforma un grupo independiente en el extremo negativo de la primera coordenada y positivo de la segunda coordenada.

Discusión

Polypogon aparece desde el punto de vista micromorfológico de la epidermis de la lemma, como un grupo heterogéneo, observándose dos grupos principales. El primero, que incluye a la sección *Polypogon* (*P. australis*, *P. interruptus*, *P. monspeliensis*, *P. linearis* y *P. viridis*) muestra la epidermis de la lemma sin malla y células largas con paredes anticlinales, en general, rectas. El segundo grupo incluye a la sección *Polypogonagrostis* (*P. elongatus*, *P. exasperatus*, *P. chilensis* y *P. imberbis*), que muestra la epidermis de la lemma con malla y células largas con paredes onduladas en U. Estos grupos se separan claramente en los análisis de conglomerados y de coordenadas principales (Figs. 8–9).

En general, la sección *Polypogonagrostis* comparte con *Agrostis* la presencia de malla. La malla ha sido considerada un carácter de valor taxonómico importante para distinguir la sección *Polypogonagrostis* de la sección *Polypogon* (Müller 1985) o para reconocer a *Chaetotropis* como un género distinto de *Polypogon* (Nicora & Rúgolo de Agrasar 1987), así como para distinguir *Agrostis* de *Polypogon* s.s. (Rúgolo de Agrasar & Molina 1997a). En general, nuestros resultados coinciden con la observación de Rúgolo de Agrasar & Molina (1997a), en que la malla permite la separación de *Polypogon* s.s. y *Agrostis*, con la excepción de *A. magellanica*, *A. kuntzei* y *A. philippiana*, que no muestran malla sino células largas no engrosadas con paredes anticlinales profundamente onduladas.

Nicora & Rúgolo de Agrasar (1987) destacan que algunas especies de *Agrostis* como *A. magellanica* son problemáticas debido a su similitud con *Chaetotropis*. La principal diferencia entre *Chaetotropis* y *Agrostis* es la desarticulación de la raquilla. En *Agrostis* típicamente desarticula sobre las glumas persistiendo éstas en la planta después de desprendidos los antecios, mientras que en *Chaetotropis* las espiguillas caen completas llevando una parte o todo el pedicelo (Rúgolo de Agrasar 1982). Por otra parte, las especies de *Agrostis* y *Chaetotropis* comparten la presencia de malla en la epidermis de la lemma. Si bien *A. magellanica* y *A. kuntzei* se acercan a *Chaetotropis* por la desarticulación de la raquilla, ambas especies muestran ausencia de malla. La epidermis de la lemma en estas especies presenta células largas con paredes anticlinales profundamente onduladas, carácter compartido únicamente por ×*Agropogon lutosus*. De acuerdo con Rúgolo de Agrasar & Molina (1997b), éste carácter acerca ×*Agropogon* a *Polypogon*, no obstante, en *Polypogon* s.s. la epidermis de la lemma posee células largas con paredes anticlinales rectas o con tenues ondulaciones, nunca profundamente onduladas, como ocurre en ×*Agropogon* o en *Agrostis kuntzei*, *A. magellanica* y *A. philippiana*. Nuestros resultados acercan ×*Agropogon* a *Agrostis* y sitúan a *A. magellanica* y *A. kuntzei* en *Chaetotropis* (*Polypogon* sect. *Polypogonagrostis*), demostrando que el valor taxonómico de la malla es discutible a nivel genérico. Cabe señalar además, que células largas profundamente onduladas, con una conformación similar a la descrita para ×*Agropogon lutosus* se han descrito en especies del género *Lachnagrostis* Trin. (*L. billardierei* (R. Br.) Trin.) y *Deyeuxia* (*D. decipiens* (R. Br.) Vickery, *D. innominata* D.I. Morris, *D. scaberula* Vickery) (Jacobs 2001).

Soreng et al. (2003) señalan que *A. magellanica* se encuentra en una posición intermedia entre *Agrostis* y el "grupo *Chaetotropis*" de *Polypogon*. Con respecto a *A. kuntzei* señalan su posible sinonimia con *P. exasperatus*. Esta especie, transferida a *Polypogon* por Renvoize (1998) se acerca también al grupo *Chaetotropis*. Las Figs. 8 y 9 muestran ambas especies asociadas a *Chaetotropis* (=*Polypogon* sect. *Polypogonagrostis*), a pesar de carecer de malla. Otros caracteres que *A. magellanica* y *A. kuntzei* comparten con la sección *Polypogonagrostis* son la desarticulación de la raquilla, la longitud de la pálea respecto del largo de la lemma y la ausencia de aguijones en la epidermis de la lemma.

La clasificación infragenérica de las especies chilenas de *Polypogon* es la siguiente:

POLYPOGON Desf.

1. Polypogon sect. Polypogon:

Polypogon australis Brongn., Voy. Monde 2:21. 1829. Tipo: CHILE: [Concepción]: près de la ville de la Conception, *Lesson*, ene 1825.

Polypogon interruptus Kunth, Nov. Gen. Sp. 1:134, t. 44. 1816. Tipo: [VENEZUELA]: Crescit in sylvis opacis Orinocensibus prope Atures, Rio Cataniapo et speluncam Ataruipe, *Humboldt & Bonpland s.n.*

Polypogon linearis Trin., Linnaea 10(3):301. 1836. Tipo: CHILE: Chile boreal in campis ad Concón' *Poeppig s.n.*

Polypogon monspeliensis (L.) Desf., Fl. Atlant. 1:67. 1798. Basiónimo: *Alopecurus monspeliensis* L., Sp. Pl. 1:61. 1753. Tipo: EUROPA.

Polypogon viridis (Gouan) Beistr., Bull. Soc. Bot. France 110 (89 Sess. Extraord.):56. 1966. Basiónimo: *Agrostis viridis* Gouan, Hortus Monsp. 546. 1762. Tipo: FRANCIA.

2. Polypogon sect. Polypogonagrostis Asch. & Graebn., Syn. Fl. 2:163. 1899.

Polypogon chilensis (Kunth) Pilg., Repert. Spec. Nov. Regni Veg. 16:386. 1920. Basiónimo: *Chaetotropis chilensis* Kunth, Revis. Gramin. 1:272, t. 47. 1830. Tipo: [CHILE]: Crescit in regne chilense, *d'Urville s.n.*

Polypogon elongatus Kunth, Nov. Gen. Sp. (quarto ed.) 1:134-135. 1816. Tipo: [ECUADOR]: Crescit in temperatis regni Quitensis prope Chillo, alt. 1350 hexap., floret aprili, *Humboldt & Bonpland s.n.*

Polypogon exasperatus (Trin.) Renvoize, Gram. Bolivia 235. 1998. Basiónimo: *Agrostis exasperata* Trin., Mem. Acad. Imp. Sci. Saint-Petersbourg, Ser. 6, Sci. Math., Seconde Pt. Sci. Nat. 4:352. 1841. Tipo: CHILE: Concepción, *d'Urville s.n.*

Polypogon imberbis (Phil.) Johow, Est. Fl. Islas de Juan Fernández 136. 1896. Basiónimo: *Nowodworskya imberbis* Phil. Anales Univ. Chile

43:562. 1873. Tipo: CHILE. [Juan Fernández]: Hallé esta grama en la isla de Juan Fernández a orillas del mar en el puerto del Inglés, *Philippi s.n.*

ANEXO 1

Anexo 1. Especies, localidad de origen y coleccionista de los especimenes utilizados en las observaciones micromorfológicas de la epidermis de la lemma, ordenados alfabéticamente. Los especimenes ilustrados se señalan con un asterisco (*).

xAgropogon lutosus (Poir.) P. Fourn. CHILE. Los Lagos: Osorno, Pto. Octay, playa del lago Llanquihue, 23 Feb 1989, *Rúgolo de Agrasar 1218** (SI).

Agrostis brachyathera Steud. (Fig. 1A-B). CHILE. Maule: Cauquenes, R.N. Los Ruiles, sector Tierra de Panllevar, 35°50'S, 72°30'W, 300 m, 15 Dic 1999, *Finot & López 1442** (CONC). Magallanes: Antártica Chilena, Isla Grevy, Punta Dillon, 55°30'S, 67°35'W, Ene 1982, *Pisano 5441* (CONC).

A. breviculmis Hitchc. CHILE. Bío-Bío: R.N. Ralco, faldeos del volcán Callaqui, 37°54'S, 71°23'W, 1735 m, 2 Ene 2002, *Mihoc et al. 4437** (CONC); Maule: Cauquenes, Linares, fundo El Castillo, Río Blanco, 36°14'S, 71°14'W, 823 m, Mar 1999, *Ruiz & López 914** (CONC).

A. glabra (J. Presl) Kunth. CHILE. Magallanes: San Gregorio, P.N. Pali Aike, 52°05'S, 69°44'W, 170 m, 5 Ene 2002, *Dominguez 160** (CONC); Región Metropolitana: Santiago, Lo Valdés, Ene 1950, *Castillo s.n.* (CONC).

A. imberbis Phil. ARGENTINA. Mendoza: Malargüe, Paso Pehuenche, 35°57°S, 70°22°W, 2400 m, Ene 2005, *Luebert & Teillier 2310* (CONC). CHILE. Maule: Curicó, Laguna Teno, 35°10'S, 70°35'W, 2500 m, Mar 1967, *Marticorena & Matthei 898** (CONC).

A. inconspicua Kunze ex E. Desv. CHILE. Bío-Bío: R.N. Ñuble, 37°06'S, 71°10'W, 1500 m, 7 Feb 2008, *Teneb 577** (CONC); Volcán Chillán, Termas de Chillán, 36°55'S, 71°28'W, 1400 m, 22 Dic 2001, *R. Soreng & N. Soreng 7136** (CONC).

A. insularis Rúgolo & A.M. Molina. CHILE. Los Lagos: Chiloé, Isla Chaulines, 42°38'S, 73°16'W, 25 m, 20 Ene 1985, *Villagrán & Aguila 6063** (CONC); Isla Alao, lado norte, barrancos, 1985, *Villagran & Meza 5890* (CONC).

A. kuntzei Mez. CHILE. Coquimbo: Elqui, Cordillera de Ovalle, 30°39'S, 70°40'W, 2400 m, Ene 1949, *Jiles s.n.* (CONC); Limarí, Cordillera de Ovalle, La Hualtata, 30°39'S, 70°40'S, 2500 m, Ene 1947, *Jiles 1184** (CONC).

A. magellanica Lam. CHILE. Magallanes: Río Santa María, 53°40'S, 70°59'W, 10 Feb 1972, *Pisano 2527** (CONC); Lago Yulton, Ensenada Caipillán, 45°04'S, 72°51'W, 490 m, Ene 2007, *García 3958** (CONC).

A. masafuerana Pilg. CHILE. Isla Juan Fernández, 880 m, 20 Ene 1986, *Landero & Gaete 9155** (CONC).

A. mertensii Trin. CHILE. Maule: Talca, borde del río Maye, 35°44'S, 35°44'W, 1300 m, Dic 1990, *Leuenberger 4066* (CONC); Talca, R.N. Alto Vilches, 35°36'S, 71°00'W, 2000 m, Ene 2000, *Finot & López 1746** (CONC).

A. philippiana Rúgolo & De Paula. CHILE. Bío-Bío: Ñuble, Termas de Chillán, 36°54'S, 71°23'W, 1600 m, Mar 2001, *Baeza & Finot 3670** (CONC); R.N. Ralco, 37°52'S, 71°23'W, 1800 m, Ene 2002, *Mihoc et al. 4102** (CONC).

A. scabra Willd. CHILE. Araucanía: Malleco, P.N. Nahuelbuta, 37°43'S, 73°02'W, 1260 m, *Weinberger 1453* (CONC). Aysén: Aysén, lago Yulton, terraza al interior del río Maca, 45°05'S, 73°02'W, 580 m, 18 Ene 2007, *Garcia 3948** (CONC).

A. stolonifera var. *palustris* (Huds.) Farw. CHILE. Bío-Bío: Arauco, Tirúa, 38°19S, 73°29W, 90 m, *Parra & Torres 669** (CONC). Los Lagos: Chiloé, Isla Guafo, 43°36'S-74°44'W, 100 m, Feb 1986, *Villagrán & Leiva 7557** (CONC).

A. stolonifera L. var. *stolonifera*. CHILE. Tarapacá: Iquique, 72 km NE de Huara hacia Chusmiza, 19°41'S, 69°10'W, 3410 m, Mar 2001, *Peterson & Soreng 15620** (CONC). Bío-Bío: Arauco, Los Álamos, 37°42'S-73°36'W, 70 m, *Parra & Torres 555* (CONC).

Polypogon australis Brongn. CHILE. Antofagasta: Quebrada de la Vaca, 25°25´S, 70°26'W, 560 m, Sep 1941, *E. Pisano & Bravo 200** (CONC). Los Lagos: Valdivia, puente Río Cruces, 39°50´S, 73°16´W, 5m, Ene 2004, *Gardner & Knees 6974** (CONC).

P. chilensis (Kunth) Pilg. CHILE. Los Lagos: Chiloé, Lago Río Negro, 42°42´S, 72°35´W, 100 m, Ene 1986, *Villagrán et al. 6954** (CONC). Chiloé, localidad de Huildad, 43°03´S, 73°35´W, 100 m, Feb. 1983, *Villagrán 4899** (CONC).

P. elongatus Kunth. ARGENTINA. Santa Fe: La Capital, Calastiné, *Tedane 522*1* (SI). CHILE. Región de Los Lagos: Prov. Chiloé, isla Quilán, 43°24´S-74°15´W, 25 m, Feb 1986, *Villagrán & Leiva 7225* (CONC). Chiloé: trayecto caleta Santa Bárbara- Chana, 42°49´S, 72°50´W, 5 m, Ene 1986, *Villagrán et al. 7095* (CONC).

P. exasperatus (Trin.) Renvoize. ARGENTINA. Catamarca: Reserva de la Biósfera Laguna Blanca, 16 Mar 1989, *Reca & Ramadori 132* (SI). CHILE. Los Lagos: Valdivia, Panguipulli, lago Puyehue, Isla Fresia, 40°39´S, 72°25´W, 850 m, Ene 1954, *Levi 1742** (CONC). Región Metropolitana: Río Clarillo, 33°42´S, 70°33´W, 700 m, Mar 1987, *Araya 69** (CONC).

P. imberbis (Phil.) Johow. CHILE. Bío-Bío:. Arauco, Playa Quiala, 37°27´S, 73°35´W, 3 m, *Parra &. Torres 237* (CONC). Los Lagos: Chiloé, Isla Quilán, entre Puntas Mala y Abrigo, 43°24´S, 74°15´W, 20 m, Feb 1986, *Villagrán & Leiva 7280** (CONC).

P. interruptus Kunth. CHILE. Antofagasta: Vega Chaco Norte, 25°24´S, 69°13´W, 3375 m, Feb 2001, *Latorre et al 236* (CONC). Región Metropolitana: Santiago, Quebrada la Plata, 33°29´S, 70°54´W, 740 m, Nov 1960, *Schlegel 3198* (CONC).

P. linearis Trin. CHILE. Tarapacá: Iquique, Isluga, 19°15´S, 68°43´W, 3850 m, Mar 1985, *Marquet s.n* (CONC). Maule: Cauquenes, 5,8 km al sur del desvió a Sauzal, 35°48´S, 72°01´W, 125 m, Dic 1994, *Bliss & Lusk 808** (CONC).

P. monspeliensis (L.) Desf. CHILE. Maule: Curicó, 8 km norte R.N. Laguna Torca, 34°42´S, 72°02´W, 20 m, Dic 2000, *Finot & Leppe 121* (CONC). Bío-Bío: Ñuble, Bulnes, puente el Roble, 36°45'S, 72°25´W, 64 m, Dic 1967, *Parra & Rodríguez 77* (CONC); Ñuble: camino Concepción-Bulnes, fundo Chillán, 36°35´S, 72°04´W, 136 m, Dic 1987, *Olea 79* (CONC); Concepción: Talcahuano, isla Rocuant, 36°44´S, 73°03´W, 5 m, Ene 2005, *Rodríguez et al 4042* (CONC).

P. viridis (Gouan) Breistr. CHILE. Tarapacá: Antofagasta, Taltal, 25°24´S, 70°29´W, 225 m, Oct 1991, *Quezada & Ruiz 413* (CONC). Bío-Bío: Ñuble, Ninhue, San Agustín de Puñual, 36°23´S, 72°25'W, 130 m, Ene 1994, *Finot & Riquelme 733* (CONC).

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BOOK NOTICES

Ruth Kassinger. 2010. **Paradise Under Glass: An Amateur Creates a Conservancy Garden.** (ISBN13: 978-0-06-154774-4, ISBN10: 0061547743, hbk.). William Morrow Imprint, HarperCollins Publishers, 10 East 53rd Street, New York, New York 10022, U.S.A. (**Orders:** http://harpercollins.com/books/Paradise-Under-Glass-Ruth-Kassinger/?isbn=9780061547744). $24.99, 368 pp., 5½" × 8¼".

This is a chronicle of Kassinger's voyage into the world of indoor gardening. Inspired by a happenchance visit to the U.S. Botanic Gardens's conservatory, she felt that a conservatory would be the perfect antidote for her losses and the changes of middle age. Her narrative includes a history of glasshouses of the past, her dealings with characters involved with the design, construction, and the development of the enclosed garden and plants, including a pint-sized indoor pool. It is a remarkable and inspiring story of the fulfilling of a dream.

Ruth Kassinger is the author of a number of award-winning science and history books for young adults, including *Reinvent the Wheel* (2001), *Build a Better Mousetrap* (2002), and *Dyes* (2003). Her science and health writing has appeared in well known national magazines, journals, and newspapers.

MISSOURI BOTANICAL GARDEN PRESS (ST. LOUIS, MISSOURI)

Sedges (Cyperaceae)

Robert F.C. Naczi and Bruce A. Ford, Eds. 2008. **Sedges: Uses, Diversity, and Systematics of the Cyperaceae.** (ISBN 978-1-930723-72-6, hbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 108. Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $75.00, 298 pp., illus., 7" × 10".

From the Publisher: "The sedge family (Cyperaceae) is one of the 10 largest families of flowering plants, with over 5,000 species and 108 genera. Sedges grow on every continent except Antarctica. They occur in habitats ranging from marshes to deserts, and they dominate many ecosystems, including tundra and savanna. Some species are habitat-specific, narrowly distributed, and of conservation concern, whereas others are ubiquitous weeds that occur in a variety of environments. Many species fill key ecological roles, and others are economically important. Yet, sedges remain poorly known. Their reduced flowers and complicated patterns of morphologic variation make the identification of these fascinating plants challenging. As a result, many have avoided the study of sedges as too difficult."

This excellent reference book covers just about any and everything concerning the Cyperaceae: from ethnobotany to weeds and from florulas to phylogeny. The list of international contributors is impressive. Below are the contents with authors.

1. Frosted Curls to Tiger Nuts: Ethnobotany of Cyperaceae—*David A. Simpson*
2. The Significance of Cyperaceae as Weeds—*Charles T. Bryson and Richard Carter*
3. Diversity, Endemism, and Phytogeography of North American Coastal Plain Sedges—*Bruce A. Sorrie*
4. *Carex* (Cyperaceae) of the Kisatchie National Forest, Louisiana, U.S.A.—*Philip E. Hyatt*
5. Description of the Population, Canopy Cover, and Associated Vegetation of the Globally Rare Sedge *Carex polymorpha* (Cyperaceae) in Nescopeck State Park, Pennsylvania—*Jamie L. Horvath, Timothy A. Block, and Ann Fowler Rhoads*
6. Segregation of Sedge Species (Cyperaceae) Along Environmental Gradients in Fens of the Schefferville Region, Northern Quebec—*Anna Dabros and Marcia J. Waterway*
7. The Carex Flora of Quebec Labrador North of 54 degrees North—*Jacques Cayouette*
8. Allozyme Variation in the Genus *Carex*...15 Years Later: 1986 to 2001—*Leo P. Bruederle, Stephen L. Yarbrough, and Shannon D. Fehlberg*
9. Phylogeny and Patterns of Convergence in *Carex* Sect. *Ovales* (Cyperaceae): Evidence from ITS and 5.8S Sequences—*Andrew L. Hipp*
10. East vs. West: Monophyletic Clades Within the Paraphyletic *Carex acuta* Complex, Section *Phacocystis* (Cyperaceae)—*Julie A. Dragon and David S. Barrington*
11. *Carex* Sect. *Phyllostachyae*: The Value of a Multidisciplinary Approach in Conducting Systematics Studies in Sedges—*Bruce A. Ford, Robert F.C. Naczi, and Julian R. Starr*
12. Phylogeny of the Unispicate Taxa in Cyperaceae Tribe Cariceae II: The Limits of *Uncinia*—*Julian R. Starr, Stephen A. Harris, and David A. Simpson*
13. Towards a Revision of the Genus *Pleurostachys* (Cyperaceae): Preliminary Results—*William Wayt Thomas and Marccus Alves*
14. Cladistic Analysis in *Rhynchospora* Sect. *Pluriflorae* (Cyperaceae)—*Ana Claudia Araujo, William Wayt Thomas, and Hilda M. Longhi Wagner*

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CARACTERIZACIÓN Y USO DE "PIMIENTAS" EN UNA COMUNIDAD QUILOMBOLA DE LA AMAZONÍA ORIENTAL (BRASIL)

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RESUMEN

Este estudio tuvo como objetivo evaluar la diversidad de las "pimientas" en la comunidad quilombola de cuatro localidades del Área de Protección Ambiental del Río Curiaú (Amapá, Brasil), a fin de lograr su caracterización taxonómica y sus usos tradicionales. Se realizaron entrevistas semi-estructuradas, con 16 especialistas locales, mediante los cuales en cada especimen citado se verificó su presencia y uso local. Se elaboró una clave diferencial de las especies, las que son detalladamente descriptas e ilustradas. Se registraron 22 etnoespecies y siete taxones: *Piper tuberculatum* Jacq. y *P. marginatum* Jacq. (Piperaceae); *Capsicum annuum* L. var. *annuum* and var. *glabriusculum* (Dunal) Heiser & Pickersgill, *C. chinense* Jacq., *C. baccatum* var. *umbilicatum* (Vell.) Hunz. et Barboza, and *C. frutescens* L. (Solanaceae). La "pimenta malagueta" (*C. frutescens*) fue la más reportada para el tratamiento de enfermedades, especialmente de la piel, además de sus indicaciones en practicas mágico-simbólicas. Los especialistas entrevistados demostraron un buen conocimiento sobre la utilización de estas especies como recursos medicinales, lo que constituiría una estrategia alternativa para su conservación.

ABSTRACT

The aim of this study was to evaluate the diversity of "peppers" in the "quilombola" community within four regions of the Área de Protección Ambiental do Río Curiaú (Amapá, Brazil), in order to profile the taxonomy and traditional uses of the species. Semi-structured interviews were conducted, with 16 experts in their respective "peppers" homegardens, where both the presence of each specimen and its local use were verified. A key and detailed descriptions and illustrations of the species examined were developed. Seven taxa and 22 ethnospecies were recorded: *Piper marginatum* Jacq., *P. tuberculatum* Jacq. (Piperaceae); *Capsicum annuum* L. var. *annuum* and *C. annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill, *C. chinense* Jacq., *C. baccatum* var. *umbilicatum* (Vell.) Hunz. et Barboza, and *C. frutescens* L. (Solanaceae). Among ethnospecies, "pimenta malagueta" (*C. frutescens*)—in addition to its magical and symbolic attributes—was the species most commonly used for the treatment of diseases, especially skin disorders. Experts have demonstrated extensive knowledge of the use of these species as medicinal resources, and this may be an alternative strategy for the conservation of such species and/or their varieties.

INTRODUCCIÓN

La conservación de la biodiversidad necesariamente involucra aspectos biológicos, además de sociales y culturales, que ciertamente, proveen el conocimiento de las culturas locales que son fuertes elementos para su conservación (Albuquerque 2005).

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La etnobotánica, ciencia interdisciplinar, es responsable del estudio de las sociedades humanas y sus interacciones ecológicas, simbólicas y culturales con las plantas. Albuquerque (1997) define la etnobotánica como el estudio de la interrelación directa entre los seres humanos de culturas vivientes y las plantas de su medio, sumado a los factores culturales y ambientales, las concepciones desarrolladas por esas culturas sobre las plantas y el aprovechamiento que se hace de ellas. La etnobotánica emplea los conocimientos tradicionales con el propósito de analizar prácticas comunitarias para fines conservacionistas y, tanto la etnobotánica como la etnobiología, son ciencias que hoy han sido bastante utilizadas para estudiar usos y manejos de los recursos naturales a través del conocimiento local de las comunidades llamadas tradicionales (Diegues 2004).

El saber ecológico es un cúmulo de conocimientos y creencias, pasado a través de generaciones por transmisión cultural, acerca de la relación de los seres vivos con su ambiente (Posey 2000). Designamos "saber ecológico local" a las experiencias cotidianas, tradicionales o no, de recolección y manejo de las especies y/o etnoespecies vegetales realizados por los pueblos tradicionales, adquiridas a lo largo de los años, y generalmente registradas por especialistas locales que acumulan informaciones sobre la utilización de las especies en la comunidad a lo largo del tiempo (Pereira 2004).

El concepto de etnogénero y etnoespecie se refiere a agrupaciones de taxones en categorías taxonómicas etnobiológicas genéricas y específicas respectivamente, y que puede ser homologable o no a las categorías de la taxonomía científica lineana; éstos se definen por criterios taxonómicos y lingüísticos y se ordenan jerárquicamente de manera tal que los taxones de cada grado jerárquico resulten mutuamente excluyentes (Martin 1995). El etnogénero es la categoría más relevante en la botánica tradicional. Sus nombres son los primeros que aprenden los niños y se mencionan con frecuencia en las entrevistas e inventarios etnobotánicos; son muy numerosos y se reconocen fácilmente, contando por lo general de un nombre primario (o semánticamente unitario ej: "maní," "pimenteira"). En tanto, las etnoespecies se corresponden por lo general con un nombre secundario (o expresión semántica binaria que contiene y nombra a la categoría más elevada acompañada de un modificador; ej: "pasto limón"; "pimenta malagueta").

El conocimiento sobre uso y cultivo de especies de las "pimientas" en Brasil es una realidad (Barbosa et al. 2002; Manara et al. 2009); sin embargo, desde el punto de vista conservacionista, poco se sabe sobre la forma en que esas especies son manejadas y/o cultivadas, necesitando de una evaluación de los mecanismos de recolección y domesticación de las especies en quintas (= quintas florestales) en la Amazonía (Barbosa et al. 2002; Nascimento-Filho et al. 2007).

En Brasil, las "pimientas" están distribuidas por todo el territorio nacional y poseen importancia económica y medicinal (Pio Corrêa 1984; Souza & Lorenzi 2005). Pertenecen a las más variadas familias botánicas, destacándose las siguientes: "pimenta de áfrica" – *Xylopia aethiopica* (Dunal) A. Rich. (Annonaceae), "pimenta rosa" – *Schinus terebinthifolius* Raddi (Anacardiaceae), "pimenta-da-jamaica" – *Pimenta dioica* (L.) Merr. (Myrtaceae), "pimentera" – *Trichilia quadrijuga* Kunth ssp. *quadrijuga* (Meliaceae), "pimentera" – *Cinamodendron dinissi* Schwacke (*Capsicodendron dinissi* (Schwacke) Occhioni, Canellaceae), "pimenta-de-cobra" – *Piper cernuum* Vell. (Piperaceae), "cumari-do-pará" – *Capsicum chinense* Jacq. (Solanaceae), entre otras.

En la región Amazónica, las "pimientas" tienen un papel importante en la vida cotidiana, en especial en la alimentación, en las representaciones mágico-simbólicas contra las llamadas "enfermedades del alma" y para las más diversas enfermedades corporales. De muchas de esas indicaciones terapéuticas citadas por gran parte de las comunidades tradicionales, su eficacia medicinal ha sido comprobada por la comunidad científica, y son comercializadas por la industria farmacéutica mundial (Manara et al. 2009). Algunas de las especies arriba citadas no son conocidas popularmente en el Estado de Amapá como "pimientas," a pesar de que la población local usa y cultiva varias de ellas.

Las "pimientas," particularmente las del género *Capsicum*, cuando son plantados en otros ambientes ajenos a su hábitat natural, pueden modificarse por hibridación genética, transformándose en variedades con características morfológicas totalmente diferentes de las originales (Carvalho et al. 2006) o en respuesta a su plasticidad fenotípica ante diferentes condiciones de cultivo (Chies & Longhi-Wagner 2003). Por esta razón,

varios taxones que fueron citados por los especialistas locales, al presentar características muy diferentes o muy semejantes, causaron cierta confusión en el momento de su determinación taxonómica.

Frente a esta realidad, se pretende estudiar la diversidad y la taxonomía de las "pimientas" usadas y manejadas en las quintas de especialistas locales de cuatro localidades del Área de Protección Ambiental del Rio Curiaú a fin de definir la identidad de las especies que aparecen en el área de estudio y sus respectivas indicaciones de usos.

MATERIALES Y MÉTODOS

Área de estudio

El área de Proteccíon Ambiental del Rio Curiaú (APARC), creado por decreto en 1992, se encuentra a 11 km de la ciudad de Macapá, capital de Amapá, entre los paralelos 00° 00'N, 00° 15'N y el meridiano 51° 00'W (Fig. 1). Posee un área de 3268,94 km^2 y una población cercana a 1500 habitantes distribuidos en seis localidades (Extrema, Mocambo, Curiaú de Fora, Curiaú de Dentro, São Francisco da Casa Grande e Curralinho). A través de una exploración previa, se pudo determinar que solamente los pobladores de Curiaú de Fora, Curiaú de Dentro, São Francisco da Casa Grande y Curralinho tienen el hábito de cultivar y emplear diferentes "pimientas," por lo que se seleccionaron estas localidades para este estudio.

Los lugares estudiados poseen un edificio de iglesia católica, la sede de una asociación de vecinos con teléfonos móviles, fijo y público, electricidad, servicio de tratamiento de agua corriente, recolección de basura con la ausencia de tratamiento de aguas residuales y, sólo en Curiaú de Dentro existe un centro de salud, una comisaría y una escuela primaria y secundaria.

Aspectos etnohistóricos locales

En Brasil, existen más de 200 grupos étnicos (Brasil 1998), entre los que se encuentran los establecimientos de comunidades tradicionales no indígenas afro-descendientes, que integran los "quilombos" (Diegues & Arruda 2001). Los quilombolas son descendientes de los esclavos negros que, por lo general, viven de actividades relacionadas a la agricultura familiar, la artesanía, la recolección y la pesca, según sea la región en la que habiten (Diegues & Arruda 2001); sobreviven en una cultura de subsistencia, con manifestaciones culturales que tienen un fuerte vínculo con el pasado (Queiroz 1997). Brasil cuenta con unas 4000 comunidades quilombolas que surgieron en granjas en bancarrota, o por donaciones de tierras a los ex-esclavos, o en terrenos adquiridos por los esclavos liberados, o en tierras concedidas a cambio de los servicios de los esclavos durante la guerra (IBASE 2006; Crepaldi & Peixoto 2009).

La comunidad de Curiaú, así llamada por la mayoría de los residentes, es considerada un sitio histórico, con su población formada por negros que huyendo de los malos tratos a los que fueron sometidos durante la construcción de la Fortaleza de San José de Macapá, en 1760, se refugiaron en un área que se denominó "quilombo" (Silva 2002; Marin 1997).

La historia de la formación étnica de Curiaú encuentra apoyo tanto en narrativas transcritas por estudiosos como en las documentaciones que datan de los siglos XVIII y XIX, existentes en los archivos públicos del estado de Pará y de la Guiana Francesa. Tales documentos atestan que en la década de 1760 se dio inicio a la entrada de esclavos para los trabajos de la Fortaleza, de las construcciones de las Villas de Macapá y Mazagão (municipios del estado del Amapá) y para los trabajos de la agricultura comercial con el cultivo de arroz y de algodón (Marin 1997; Rodrigues 2010). Otra versión, es la citada por Silva (2002) y Brito & Drummond (2007) quienes en un estudio en la comunidad de la APARC y, basados en testimonios de los habitantes más antiguos, afirman que los esclavos africanos, enojados por los malos tratos sufridos en la construcción de la fortaleza, huyeron y se escondieron en la región bajo el amparo de un señor, el Sr. Miranda, quien se había establecido previamente con su esposa y esclavos. El señor Miranda los acogió, dándoles protección y lugar para vivir libres. Con el pasar del tiempo continuaron recibiendo a otros esclavos fugitivos, construyendo el quilombo. En la actualidad, gran parte de la población de la APARC tiene un alto grado de parentesco lo que contribuye en parte a la preservación de los aspectos culturales del lugar. Una de esas manifestaciones de la comunidad es la danza del "Marabaixo," que hoy es una de las principales fiestas

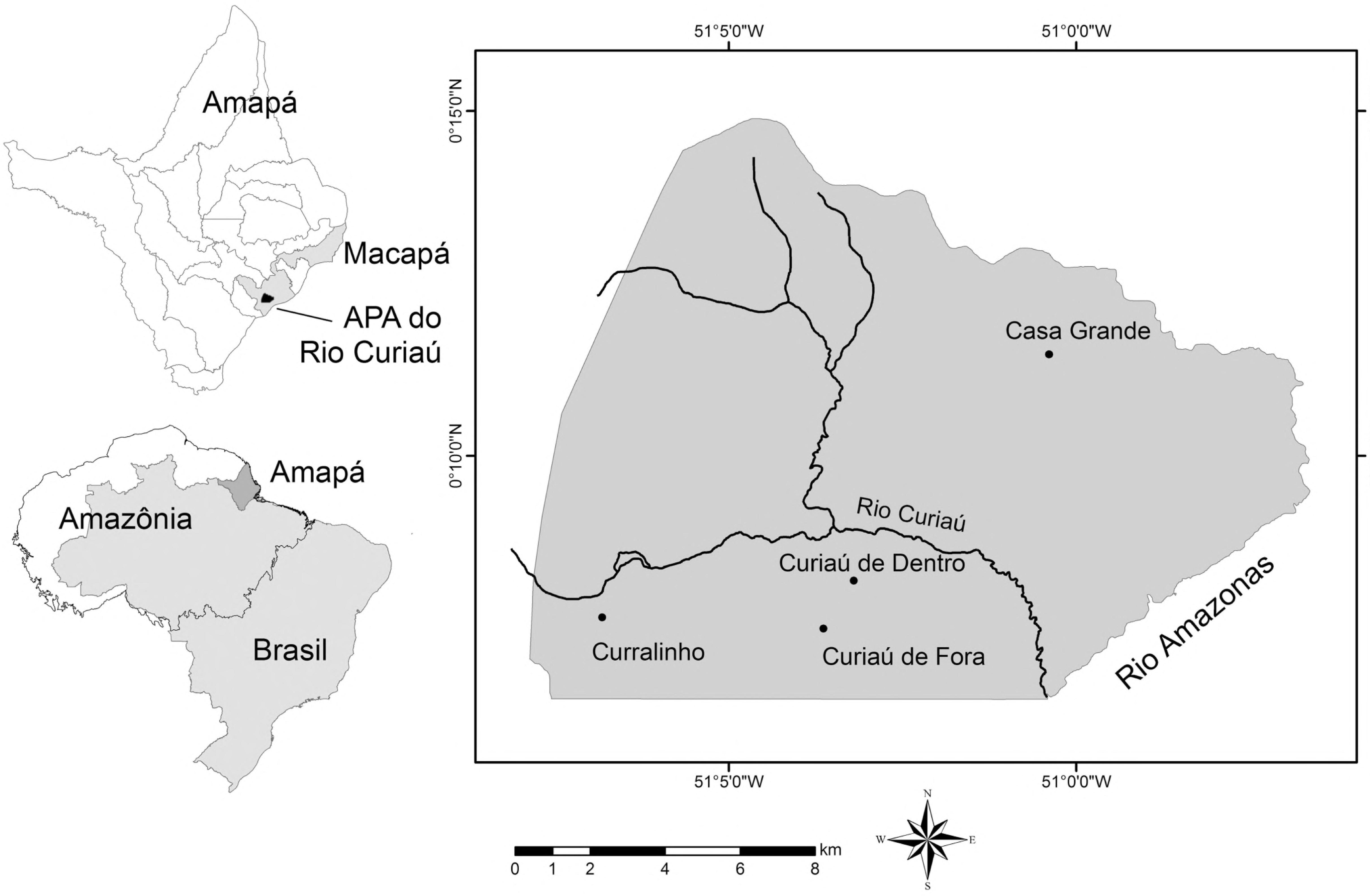

Fig. 1. Mapa de localización del área de estudio de la APA de Rio Curiaú, municipio del Macapá, Amapá, Brasil.

del estado de Amapá (Rodrigues 2009), pues reúne gran parte de los quilombolas tanto de Curiaú, como de otros lugares del Estado. Es un ritual de origen africano que se realiza durante las conmemoraciones de la Semana Santa, a partir del Domingo de Pascua hasta el domingo del Divino Espíritu Santo. La danza y el canto de "Marabaixo"constituyen el lado profano de las festividades en homenaje a la Santísima Trinidad y al Divino Espíritu Santo. Durante los festejos, se efectúa una gran distribución de una bebida denominada "gengibirra," formada por una mezcla de gengibre, azúcar y limón, así como un caldo caliente consistente en bastante agua, carne de ganado cortada en pequeños pedazos y especias, acompañados de salsa de "tucupi" (líquido amarillo resultado de la fermentación de raíz de "mandioca") con "pimenta malagueta" o "pimenta-de-cheiro-tacacá" (*Capsicum* spp.), sal y ajo.

Recopilación de datos y toma de muestras

Las plantas fueron recolectadas en las quintas de los especialistas locales usando la técnica "turné-guiada" (Albuquerque 2005), que consiste en una caminata con el informante más calificado (= especialista), recolectando todas las especies útiles existentes y anotando las informaciones brindadas. La elección de los informantes se hizo partiendo de una primera entrevista con el informante clave (líder de la comunidad que conoce en profundidad a la mayoría de los residentes y la cultura local); luego, se utilizó el método "bola de nieve" (Bailey 1982), es decir la primera persona contactada por indicación del líder sugiere el nombre de otro informante quien, a su vez, va indicando otros nombres a ser entrevistados; todos estos informantes son los llamados en este trabajo especialistas locales.

Las plantas citadas por los especialistas locales fueron ubicadas en seis categorías de usos, a saber: repelente, alimenticia, comercial, medicinal, ornamental y ritualística. Los especímenes fueron fotografiados, prensados y deshidradatos en estufas a 70°C, por 72 horas. El material fue estudiado con auxilio del

microscopio estereoscópico Leica MZ75, acoplado con cámara clara y procesados a través del método usual en taxonomía (Fidalgo & Bononi 1984). El material comprobatorio fue depositado en los Herbarios BHCB, CORD, HAMAB, HB, MBML y RB, siglas según Thiers (2010); material de referencia de otras localidades también fue analizado, cuando necesario, en el herbario del Museo Botánico de Córdoba (CORD, Argentina). Además, fue elaborada una clave analítica de los taxones estudiados, para su reconocimiento. Para la distribución biogeográfica de las especies, se han seguido los conceptos de Cabrera & Willink (1980) y Cavalcante & Major (2006).

RESULTADOS Y DISCUSIÓN

Diversidad y taxonomía de las "pimientas"

Los resultados indican que, a pesar del gran número de etnoespecies citado en las entrevistas por los especialistas (22 etnoespecies), no hubo un aumento considerable en el número de especies cultivadas en las quintas (siete especies); sólo se observó la adición de nuevos nombres populares para la mayoría de las especies (Tabla 1).

Un informante calificado o especialista local aplica claramente distintos nombres a los diferentes morfotipos que identifican cada etnoespecie, es decir que un único informante reconoce etnoespecies pertenecientes a una misma especie botánica. No hubo diferencias significativas entre los informantes de una misma comunidad ni entre comunidades distintas ya que en general, los especialistas consultados tienen un conocimiento arraigado de las "pimientas" y de sus usos.

Para el 75% de los especialistas locales (12), todos los nombres populares por ellos citados aluden a diferentes morfotipos, cuyas variaciones se centran principalmente en la morfología de los frutos (tamaño, forma y colores). Así por ejemplo, para "pimienta" (*Capsicum frutescens*), la población local, como en otras regiones de Brasil, utiliza el tamaño del fruto como un carácter importante para la determinación de las etnoespecies "pimenta malaguetinha" (fruto pequeño) o "pimenta malaguetão"(fruto grande). En cambio, las etnoespecies (Tabla 1) que corresponden a *C. chinense* presentaron morfología carpológica muy diversa en relación con las descripciones existentes en la literatura (Reifschneider 2000; Barbosa et al. 2006), si bien nuevos tipos son obtenidos por hibridación natural en el campo o por diferentes ambientes de cultivo (Carvalho et al. 2006). Tales variaciones dificultaron asociar la etnoespecie recolectada en las quintas con su nombre científico, por lo que se hizo un estudio más detallado "*in situ*" en la época de floración. De esta manera, se logró constatar que a pesar de las diferentes formas, tamaños y colores que presentan estas etnoespecies, todas corresponden a una misma especie (*C. chinense*).

La denominación de las etnoespecies acorde a las características morfológicas que presentan en determinadas localidades fue confirmada por Nascimento-Filho et al. (2007) en una encuesta llevada a cabo en el estado de Roraima (Brasil). Los autores afirmaron que de 180 "pimientas" en el campo (163 cultivadas y 17 nativas), 78 morfotipos difieren por la forma, color y grado de pungencia. Estos morfotipos fueron atribuidos a *C. annuum*, *C. baccatum* var. *pendulum*, *C. chinense* y *C. frutescens*, siendo los predominantes la "pimenta malagueta" (*C. frutescens*), la "pimenta murupi" (*C. chinense*) y la "pimenta-olho-de-peixe" (*C. chinense*). Estos resultados coinciden con los encontrados en este trabajo donde *C. frutescens* y *C. chinense* fueron las especies mayormente citadas por los quilombolas de Curiaú (Tabla 2).

En el área estudiada en el Área de Protección Ambiental (APA) del Curiaú se registraron siete taxones (cinco especies y dos variedades) pertenecientes a Piperaceae y Solanaceae (Tabla 1), a saber: *Piper marginatum* Jacq. (Fig. 2C), *P. tuberculatum* Jacq. (Fig. 2D), *Capsicum annuum* L. var. *annuum*, *C. annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill (Fig. 3), *C. chinense* Jacq. (Fig. 4A–C, Fig. 2 A), *C. frutescens* L. (Fig. 4 D–G) y *C. baccatum* var. *umbilicatum* (Vell.) Hunz. et Barboza (Fig. 2B). Únicamente las dos especies de *Piper* crecen en forma espontánea en los bosques del área estudiada (Pereira et al. 2007); ambas especies fueron citadas por dos de los 16 especialistas entrevistados y sólo como planta medicinal (Tabla 2).

Tabla 1. Lista de las "pimientas" del APA del Río Curiaú (Macapá, Amapá, Brasil) y su lugar de cultivo.

Familia	Taxones	Nombre vernacular de las etnoespecies	Lugar de cultivo Quintas	Bosque circundante
Piperaceae				
	Piper marginatum	pimenta-do-mato o malvarisco	X	X
	Piper tuberculatum	pimenta-de-macaco o pimenta longa	X	X
Solanaceae				
Capsicum annuum var. *annuum*		pimentão, pimenta-de-cheiro-ardosa	X	-
	C. annuum var. *glabriusculum*	pimenta-de-mesa, pimenta açaí, pimenta-peito-de-moça, pimenta-ova-de-aruanã, pimenta-ova-de-tamuatá, pimenta chumbinho	X	-
	C. baccatum var. *umbilicatum*	pimenta-de-cheiro-amarela	X	-
	Capsicum chinense	pimenta-amarela-ardosa, pimenta-amarela-de-cheiro, pimenta camapú, pimenta-de-cheiro-tacacá, pimenta-de-cheiro-de-panela, pimenta-de-cheiro-redondinha-ardosa	X	-
	Capsicum frutescens	pimenta malagueta, pimenta malaguetão, pimenta malaguetinha	X	X

CLAVES PARA LOS GÉNEROS DE LAS "PIMIENTAS"

1. Arbustos con inflorescencias multifloras dispuestas en espigas; flores aclamídeas; carpelos 1; fruto drupa ________ **Piper**
1. Hierbas o subarbustos, con (1–)2–4 flores axilares en fascículos; flores diclamídeas, carpelos 2 (raro 3–4-carpelar); fruto baya ________ **Capsicum**

1. PIPERACEAE

Piper L., Sp. Pl. 1:28. 1753.

Subarbustos o arbustos, árboles pequeños, 1–10 m de alt. **Tallo** con ramas nudosas, profilo generalmente caduco. **Hojas** alternas, simples, enteras, sésiles o pecioladas; pecíolo provisto de vainas cortas, alargadas o canaliculadas; nerviación predominante camptódromo-acródromo o broquidódromo, nervaduras secundarias en número variable. **Espigas** o racimos opuestos a las hojas, erectos o curvos, obtusos o apiculados, raquis sulcado, liso, papiloso o fimbriado; bractéolas peltadas, redondeadas, triangulares, semi-lunares o calciformes, de márgenes lisas o fimbriadas. **Flores** sésiles o pediceladas, aperiantadas, aclamídeas; estambres 2–6; ovario súpero obovoide a ovoide, vistoso o no, sésil o no, estigmas 3–4. **Drupas** con pericarpo delgado, con estigma persistente.

Género pantropical con especies dioicas o monoicas para el Viejo Mundo y hermafroditas en América (Tebbs 1993). Con gran distribución en las regiones tropicales y templadas de los dos hemisferios. En Brasil, habitan cerca de 266 especies (Guimarães & Giordano 2004).

La "pimenta-do-reino" (*Piper nigrum* L.), en el área de estudio no fue registrada. Es la especie económicamente más importante de Piperaceae, cultivada por los agricultores en diversas partes del mundo con numerosas variedades para la producción de la "pimienta"; se usa ampliamente como condimento además de medicinal (Tebbs 1993; Guimarães & Monteiro 2006).

CLAVE PARA LA IDENTIFICACIÓN DE LAS ESPECIES DE *PIPER* L. RECOLECTADAS EN EL ÁREA DE ESTUDIO

1. Lámina foliar palmatinervada con base simétrica y cordada, margen densamente ciliado ____________ **P. marginatum**
1. Lámina foliar penninervada con base asimétrica no cordada, margen eciliada ____________ **P. tuberculatum**

Tabla 2. Lista de las "pimientas" del APA del Río Curiaú (Macapá, Amapá, Brasil), su hábitat, grado de ocurrencia, nivel de domesticación y uso. Abreviaturas. Localidades: **CF**= Curiaú de Fora, **CD**= Curiaú de Dentro, **CG**= Casa Grande y **CR**= Curralinho; Grado de ocurrencia: **Ab**= Abundante, **Ba**= Poco abundante; Nível de la domesticación: **Si**= silvestre, **Do**= domesticada, **Se**= semidomesticada; Uso: **Me**= medicinal, **Al**= alimenticia, **Co**= comercial, **Or**= ornamental, **Re**= repelente, **Ri**= ritualística.

Familias/Taxones	Localidad cultivada/ cantidad de registros en quintas por localidad				Grado de ocurrencia		Nivel de domesticación*			Uso					
	CF	CD	CG	CR	Ab	Ba	Si	Do	Se	Al	Co	Me	Or	Re	Ri
Piperaceae															
Piper marginatum	-	2	-	-	X	-	X	-	-	-	-	X	-	-	-
Piper tuberculatum	-	2	-	-	X	-	X	-	-	-	-	X	-	-	-
Solanaceae															
Capsicum annuum var. *annuum*	1	-	-	-	-	X	-	X	-	X	X	-	-	-	-
C. annuum var. *glabriusculum*	1	-	-	-	-	X	-	-	X	X	X	X	X	-	-
C. baccatum var. *umbilicatum*	1	-	-	-	-	X	-	-	X	X	X	-	X	-	-
Capsicum chinense	2	1	-	-	X	-	-	X	-	X	X	X	X	-	-
Capsicum frutescens	4	4	3	4	X	-	-	X	-	X	X	X	X	X	X

* Adaptado de Carvalho et al. (2006)

Piper marginatum Jacq., Icon. pl. rar. 2(2), t. 215. 1789. (**Fig. 2C**).
Subarbustos o arbustos hasta 5 m alt. Hojas con láminas ovado-redondeadas, membranáceas, glabras, de 10–20 × 7–15 cm, palmatinervadas (nervios 9–11 pares, libres o, a veces, con un par de nervios laterales coalescente a la nervadura principal), base simétrica y cordada, ápice agudo o acuminado, margen densamente ciliado; pecíolos de 2–6 cm de largo, vaina con alas hasta la lámina. Espigas curvas, largas, hasta 15 cm de largo; bractéolas triangular-peltadas, fimbriadas. Estambres 4–5. Drupas obpiramidales, glabras, con 3 estigmas persistentes sésiles.

Distribución geográfica.—América Central y América del Sur. En Brasil, en los Estados de Amazonas, Amapá, Pará, Ceará, Paraíba y Pernambuco.

Siguiendo a Guimarães & Giordano (2004), en el resto de la Amazonía es conocida como "caa-peba-cheirosa," "nhandi," "nhandú," "pimenta-dos-índios," "pimenta-betel" y "malvavisco," siendo usada en decocciones como antiespasmódica para afecciones del hígado y del bazo. En algunos lugares de Brasil como Ceará, sus frutos son usados como condimento sustituyendo a la "pimenta-do-reino" (*P. nigrum*). La raíz, cuando macerada, es utilizada para aliviar la picazón de las picaduras de insectos. También es empleada como masticatorio contra dolores de dientes, además de ser carminativa. Las hojas poseen dos flavonoides: vitexina y marginatoside (Tillequin et al. 1978; Maxwell & Rampersad 1988).

En Amapá y en especial en el APA del Rio Curiaú, esta especie es bastante abundante (Tabla 2). En la localidad estudiada es una etnoespecie ampliamente conocida como "malvarisco" y fue mencionada únicamente por dos especialistas de la misma comunidad con el nombre de "pimenta-do-mato" (Tabla 2). En general, se usan las hojas y los frutos; son utilizadas localmente como antiespasmódico para afecciones del hígado, del bazo, problemas intestinales y ampliamente para el tratamiento de la tos.

Material estudiado: **BRASIL. Amapá:** Laranjal do Jarí, 2 Feb 1999 (fl), *R.S.F.R.Sarquis* s.n (HAMAB n. 10070; 10071; 10072); Macapá, Comunidade Curiaú de Dentro, 15 Jun 2008 (fl) *L.A. Pereira & H.A.Batista 1857* (HAMAB); 05 Jun 2008 (fl) *L.A. Pereira et al. 1731* (HAMAB, HB, R, RB); BR 156, 20 May 1990 (fl) *Heliodore 20* (HAMAB); Fazendinha, 16 Apr 1985 (fl) *R.Nonato et al. 11* (HAMAB); Rod. Duque de Caxias, KM 9, 12 Jul 2009 (fl, fr) *L.A. Pereira 1849* (HAMAB, RB); Mazagão, estrada do Jarí, próximo à vila do Maracá, 23 Mar 2001 (fl) *L.A. Pereira & J.P.Reis 288* (HAMAB).

Piper tuberculatum Jacq., Icon. pl. rar. 2(2): t. 211. 1789. (**Fig. 2D**).
Arbustos de 2,0–2,5 cm alt., ramas pubérulas. Hojas con láminas elípticas u ovado-elípticas, papiráceo-membranáceas, brillantes, glabras en el epifilo, pubérulas en los nervios del hipofilo, de 8–12,5 × 4–6 cm,

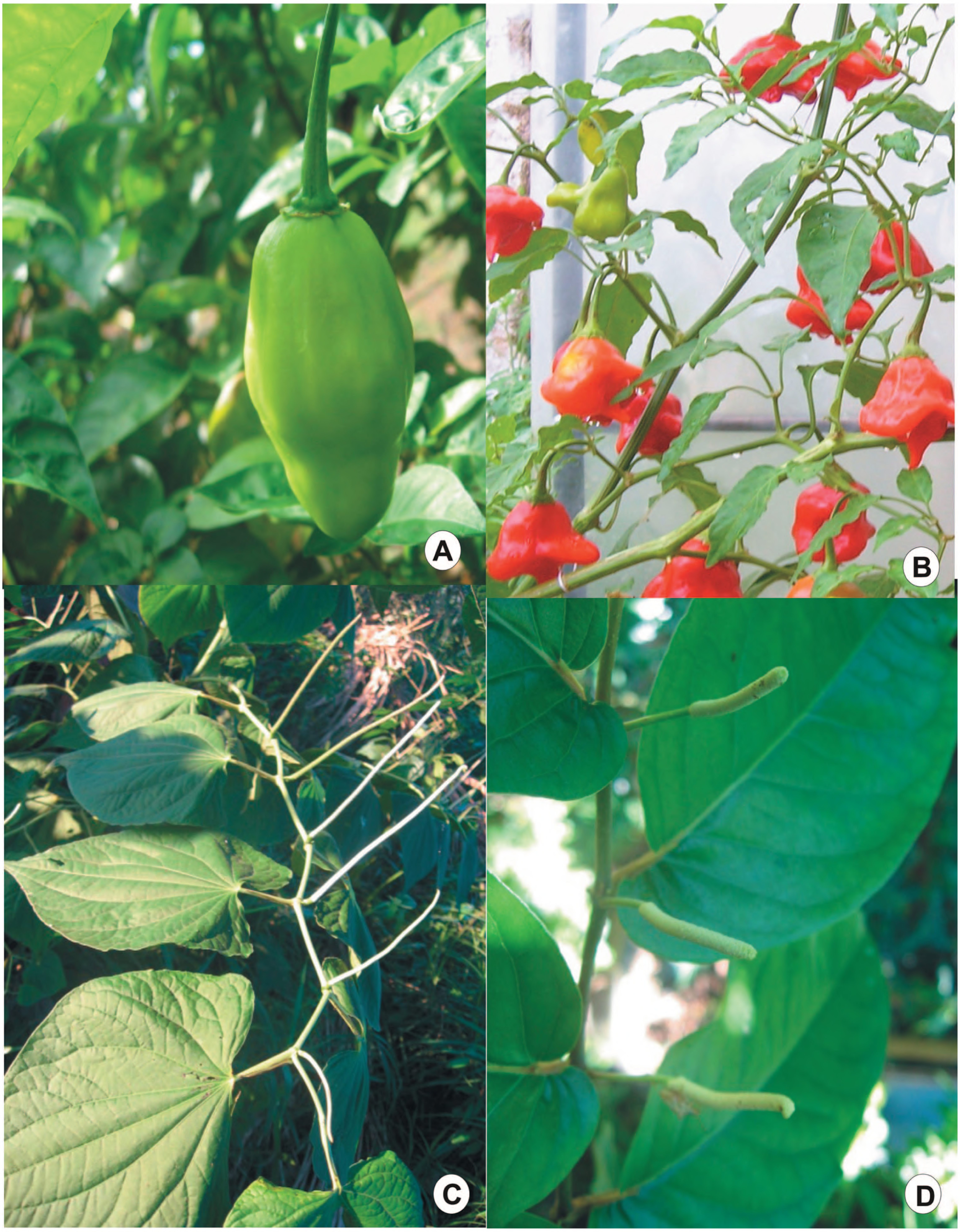

Fig. 2. A. *Capsicum chinense* (fruto péndulo); **B.** *C. baccatum* var. *umbilicatum* (rama fructífera); **C.** *Piper marginatum* (rama florífera); **D.** *Piper tuberculatum* (rama florífera).

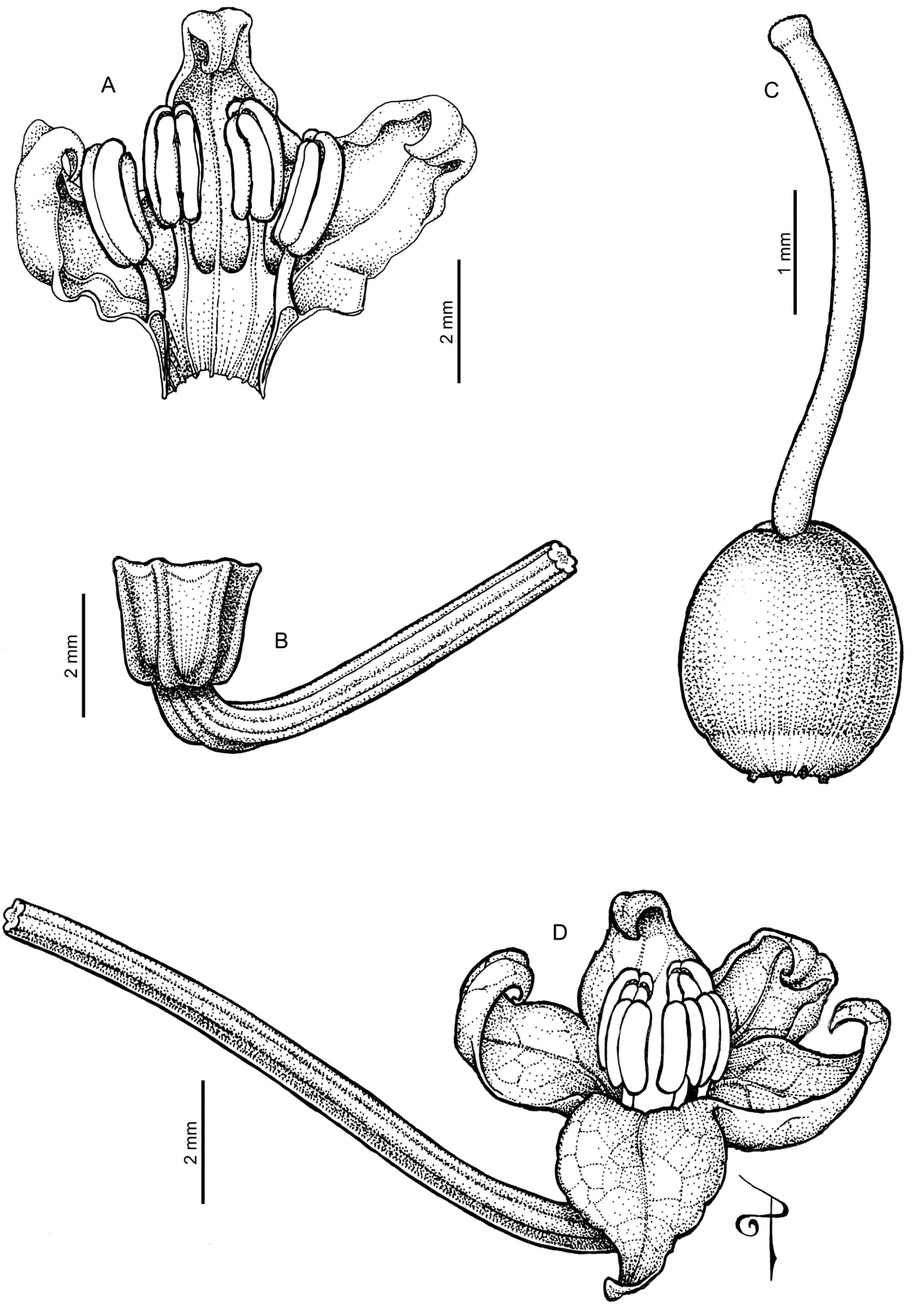

FIG. 3. *Capsicum annuum* var. *glabrisculum* (*Pereira et al. 1841*). **A.** Corola desplegada; **B.** Cáliz; **C.** Gineceo; **D.** Flor.

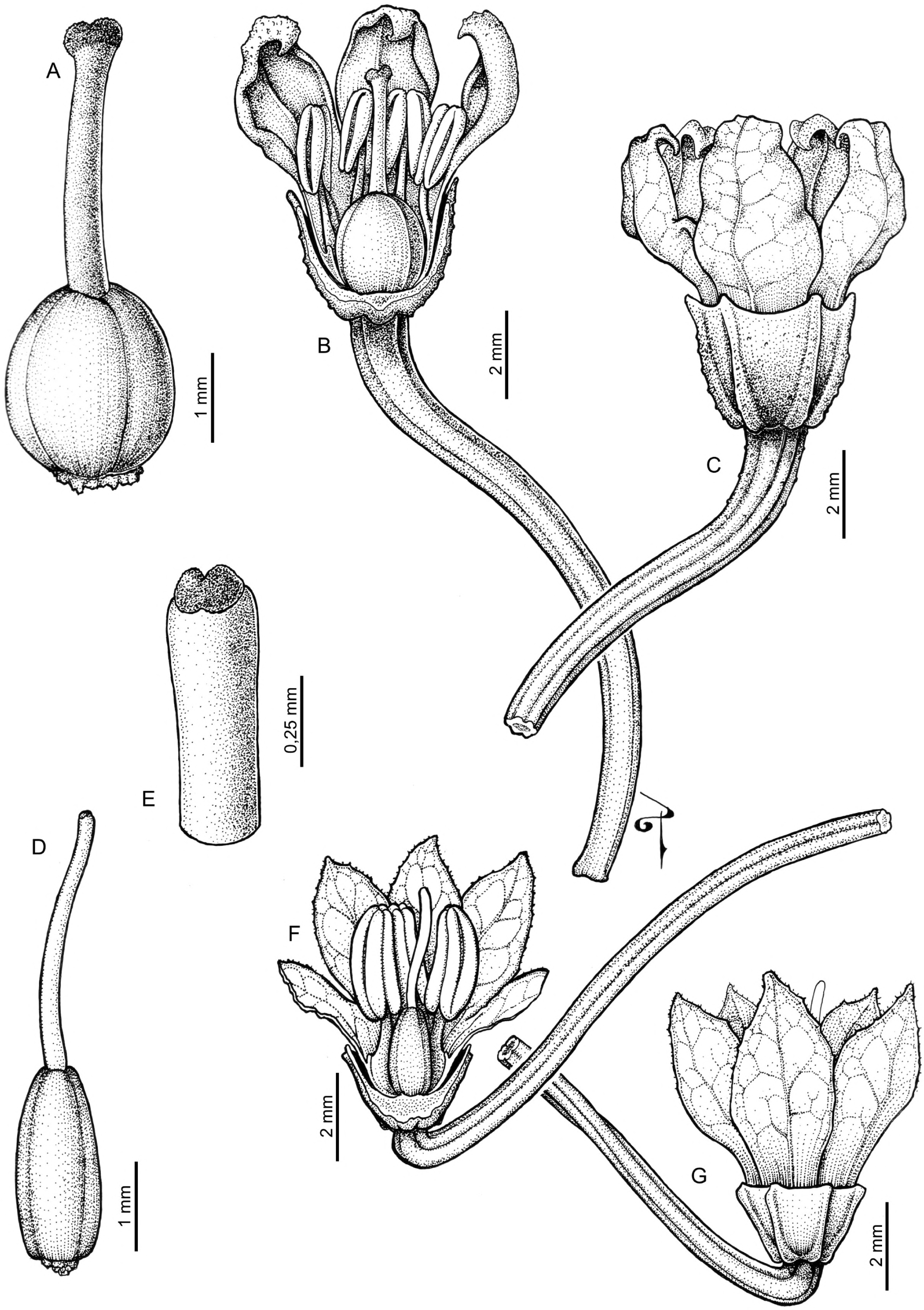

Fig. 4. A–C. *Capsicum chinense* (*Pereira et al. 1831*); **D–G.** *C. frutescens* (*Pereira et al. 1855*). **A, D.** Gineceo; **B, F.** Corola desplegada; **C, G.** Flor; **E.** Detalle del ápice estilar y estigma.

peninervadas (8–10 pares de nervios ascendentes), base asimétrica y no cordada, ápice agudo, margen eciliado; pecíolos rojos, pubérulos y papilosos, de 0,5–1,0 cm de largo, vaina con alas hasta la lámina. Espigas erectas, cortas, de 4–7 cm de largo. Estambres 4. Drupas tetragonales, ovoideas o subobovoideas, lateralmente comprimidas, glabras, con 3 estigmas persistentes sésiles.

Distribución geográfica.—Por todo el continente americano. En Brasil, ocurre en los estados de Amazonas, Amapá, Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Mato Grosso y Rio de Janeiro. Habita en áreas perturbadas de bosques abiertos (= capoeiras), principalmente, en lugares húmedos de la región biogeográfica del Cerrado (Cabrera & Willink 1980); en otras regiones de Brasil, crece en las pendientes húmedas de los bosques abiertos y en lugares pantanosos (= brejos), en altitudes aproximadas a los 550 m.

En Rio Grande del Norte se emplea como condimento. En Amapá, donde crece espontáneamente, es conocida como "pimenta-de-macaco" o "pimenta longa" (Tabla 1). En el área estudiada y en algunos otros lugares del Estado, se usa como planta medicinal, principalmente como antiespasmódica.

Material estudiado: **BRASIL. Amapá:** Macapá, 11 Jul 2001 (fl,fr), *C.Penafort & H.P.Belo 5* (HAMAB); APA do rio Curiaú, Comunidade São Francisco da Casa Grande, 7 May 2008 (fl), *L.A. Pereira et al. 1806* (HAMAB, RB).

2. SOLANACEAE

Capsicum L., Sp. Pl. 1:188. 1753.

Hierbas perennes, arbustos o subarbustos ca. 0,50–2,5(–3) m alt., glabrescentes a muy pilosos, a veces villosas. Tallos frecuentemente fistulosos, generalmente con dicotomía evidente. Hojas simples, alternas, aisladas o falsamente geminadas, pecioladas; lámina entera, ovada a estrechamente lanceolada; base abruptamente cuneada a rotunda; ápice agudo a acuminado. Flores axilares, solitarias o en fascículos, actinomorfas, pentámeras por lo general, pedicelos erectos, semi-erectos o péndulos, a veces geniculados distalmente. Cáliz persistente, truncado, con (0–)5–10 dientes o apéndices lineares, inconspicuos o muy desarrollados, iguales entre sí, que nacen por debajo del margen. Corola 5-partida en diferentes niveles, rotácea, estrellada, raramente campanulada o urceolada, íntegramente blanca, amarilla o lila, o bien blanquecina con diferentes combinaciones de manchas verdes, vináceas, amarillas y violetas; tubo pequeño, lóbulos 5 bien evidentes; estambres por lo general 5, filamentos glabros, parte basal ensanchada adherida a la corola, formando un canal nectarífero; anteras amarillas o violáceas; ovario súpero, con anillo nectarífero basal, bilocular o falsamente trilocular, óvulos 2-muchos por lóculo; estilo obsubulado; estigma pequeño, aplanado. Frutos bayas, deciduas o persistentes, cónicos, globosos u ovoides, de color amarillo, naranja, rojo, verde o verde--amarillento, brillantes u opacos, generalmente pungentes; pedicelos fructíferos erectos o pendientes. Semillas reniformes aplanadas, oscuras o claras; testa generalmente foveolada.

Capsicum es un género americano de ca. 32 especies nativas (Barboza et al. 2011). Brasil es el país con la mayor concentración de especies (Barboza & Bianchetti 2005), especialmente en la costa sureste (Est. Espírito Santo a Rio Grande do Sul), con algunos representantes en el noreste brasilero y en la Caatinga (Barboza et al. 2010).

Los frutos de la mayoría de sus especies contienen una gran variedad y cantidad de metabolitos (vitaminas, carotenoides, minerales, proteínas, carbohidratos, grasas, fibras) pero los principales componentes pungentes son la capsaicina y la dihidrocapscina (Bosland & Zewdie 2001; Manirakiza et al. 2003), los que se acumulan en la epidermis secretora del septo (Filippa & Bernadello 1992).

CLAVE PARA IDENTIFICACIÓN DE LOS TAXONES DE *CAPSICUM* L. RECOLECTADAS EN EL ÁREA DE ESTUDIO

1. Corola blanca con dos manchas amarillas o verdosas difusas en la base de cada lóbulo y parte del limbo. Gineceo con heteromorfismo estilar. Baya de coloración rojo-anaranjada, umbonado-umbilicada ______ **C. baccatum** var. **umbilicatum**
1. Corola blanca, amarillenta, verdosa o púrpura, raramente violeta; si blanca, entonces desprovista de manchas amarillentas o verdosas en la base de los lóbulos. Gineceo sin heteromorfismo estilar. Baya de coloración variada, morada, roja, amarilla, amarillo-verdosa o anaranjada, no umbonado-umbilicada.

2. Flor solitaria por nudo reproductivo. Corola a veces hasta con 7 lóbulos. Baya colgante, cuando madura amarillo-verdosa, amarilla, roja o morada oscura, ovoide a fusiforme, diámetro generalmente mayor de 3 cm ____ **C. annuum** var. **annuum**
2. Flores dos o más por nudo reproductivo. Corola 5–6 lóbulos. Baya erecta o péndula, diámetro menor de 3 cm.
   3. Flores péndulas sobre pedicelos no geniculados. Baya péndula; cáliz con constricción basal bien evidente ____ **C. chinense**
   3. Flores erectas sobre pedicelos geniculados. cáliz con constricción basal apenas evidente o ausente.
      4. Corola cremosa o amarillo-verdosa, ca. 6,5 mm de largo. Ovario y baya oblongo-ovoideos. Baya de 1,5–4 cm de largo. Cáliz cuando fructífero cupuliforme, con 5 dientes evidentes y cortos ____ **C. frutescens**
      4. Corola blanca, ca. 5 mm de largo. Ovario y baya globosos. Baya con 0,5–1 cm diám. Cáliz cuando fructífero pateliforme, mútico o con 5 dientes subapicales diminutos ____ **C. annuum** var. **glabriusculum**

Capsicum annuum L. var. **annuum** Sp. Pl. 1:188. 1753.

Subarbustos de 1–1,20 m alt. Tallos 3–4-costados, con diminuta pubescencia. Hojas verde-oscuras; láminas elípticas u ovadas, 3–6(–9) × 1,8–3cm, base atenuada y desigual, ápice acuminado, epifilo e hipofilo glabros; pecíolos de 2–6,7 cm de largo. Flores solitarias por nudo reproductivo, raramente fasciculadas; pedicelos geniculados apicalmente, erectos, de (1–)1,5–3 cm de largo, glabros a glabrescentes. Cáliz de 2,3 mm de largo, con 5 dientes subapicales diminutos. Corola blanca o amarillenta, raramente violeta, sin manchas, a veces hasta con 7 lóbulos. Estambres 5–7, anteras generalmente azuladas. Gineceo sin heteromorfismo estilar; ovario 2-carpelar. Bayas colgantes, ovoideas a fusiformes o cónicas, 2,5–4 × 1,3–2 cm., de color verde cuando inmaturas, amarillo-verdosas, anaranjadas, rojas o morado-oscuras a la madurez. Semillas discoidales, comprimidas, de color amarillo pálido, episperma finamente foveolado.

Distribución geográfica.—Ampliamente cultivada en todo el mundo.

En el área de estudio, como en otras partes del Brasil, se conoce una etnoespecie con el nombre de “pimentão” (pimiento en español), que se utiliza sólo para sazonar los alimentos y no está indicada por los especialistas ni como medicinal ni en ninguna otra categoría de uso. El nombre de esta etnoespecie se aplica por la falta de pungencia en sus frutos, usándose para dar sabor y color a las comidas. Muchas veces, otras etnovarietales como por ejemplo la “pimenta-de-cheiro-ardosa” son picantes y utilizadas solamente como condimento.

Según De (1994), algunas tribus indígenas de Brasil, utilizan los frutos en preparaciones de venenos para punta de flechas; también se usa en casos de fiebres crónicas, prácticas que no pudimos corroborar entre los quilombolas del APA del Río Curiaú.

Material estudiado: **BRASIL. Amapá:** Macapá, APA da Fazendinha, 28 May 2009 (fl), *L. Espindola-Nascimento & J.R.Pinheiro 10, 11* (HAMAB, RB); APA do Rio Curiaú, Comunidade Curiaú de Dentro, 2 May 2008 (fl,fr), *L.A. Pereira et al. 1696* (HAMAB); Comunidade Curiaú de Fora, 07 May 2008 (fl,fr), *L.A. Pereira et al. 1810* (HAMAB, RB); Santana, Ilha de Santana, 12 Jun 2008 (fl,fr) *L.A. Pereira et al. 1845* (HAMAB, HB, RB).

Capsicum annuum var. **glabriusculum** (Dunal) Heiser & Pickersgill, Baileya 19:156. 1975. (**Fig. 3**). *Capsicum hispidum* var. *glabriusculum* Dunal, Prodr. 13(1):420. 1852.

Subarbustos hasta 50 cm alt. Tallos 3–4-costados, con diminuta pubescencia. Hojas con láminas obovadas a elípticas, glabrescentes, de 4–7 × 2–2,5 cm, base atenuada y ápice acuminado; pecíolos de (0,5–)1,5–2 cm de largo. Flores por lo general 2 por nudo reproductivo; pedicelos geniculados, erectos, de 1–3 mm de largo, glabros. Cáliz de 1,3 mm de largo, glabrescente, mútico o con 5 dientes subapicales diminutos. Corola blanca, ca. 5 mm de largo. Estambres 5, anteras generalmente amarillas. Gineceo sin heteromorfismo estilar; ovario 2-carpelar, globoso, 1,2 mm diám. Bayas erectas, globosas u ligeramente ovoideas, 0,5–1 cm diám., de color amarillo oro o rojo oscuro cuando inmaturas y rojo intenso cuando maduras; pedicelo fructífero erecto, de 1,2–2,5 cm de largo; cáliz pateliforme, con constricción basal apenas evidente o ausente. Semillas discoidales, comprimidas, de color amarillo pálido, episperma foveolado.

Distribución geográfica.—Sur de los Estados Unidos, México, Bahamas, Guatemala, Belize, Nicaragua, Costa Rica, Panamá, Colombia, Venezuela, Ecuador, Perú, Bolivia y en Brasil en las regiones Norte y Nordeste. Se trata de una variedad que aún se encuentra en estado silvestre y también semidomesticada.

En el estado del Amapá y en el lugar de estudio, es conocida como "pimenta-de-mesa," "pimenta açaí," "pimenta-peito-de-moça," "pimenta-ova-de-aruanã," "pimenta-ova-de-tamuatá" y "pimenta chumbinho." Los quilombolas usan la planta como ornamental; las hojas se utilizan como medicinal para curar "furúnculos" y los frutos como condimento y con fines ornamentales. Las distintas etnoespecies mencionadas por las comunidades en estudio se refieren a la forma y tamaño de los frutos maduros que, en general, son redondeados a variadamente ovoideos y pequeños.

Material estudiado: **BRASIL. Amapá:** Macapá, APA da Fazendinha, 26 May 2009 (fr), *L. Espindola-Nascimento & L.S. Simoa 3* (HAMAB, RB); APA do Rio Curiaú, Comunidade Curiaú de Dentro, 2 May 2008 (fl,fr), *L.A. Pereira et al. 1701* (HAMAB); Comunidade Curiaú de Fora, 14 Jul 2008 (fl,fr), *L.A. Pereira & W.M.S.Severino 1853* (CEPEC, HAMAB, HB, MBML, RB); Comunidade Curralinho, 7 May 2008 (fr), *L.A. Pereira et al. 1807* (CEPEC, HAMAB, HB, MBML, RB); APA da Fazendinha, 26 May 2009 (fl,fr), *L. Espindola-Nascimento & L.S. Simoa 01, 07* (HAMAB, RB); 28 May 2009 (fl,fr), *L. Espindola-Nascimento & J.R. Pinheiro 08* (HAMAB, RB); 26 May 2009 (fl,fr), *L. Espindola-Nascimento & L.S. Simoa 02* (HAMAB, RB); Minipólo Hortifruti da Fazendinha, 8 Nov 2008 (fl,fr), *L.A. Pereira et al. 1900, 1903* (BHCB, HAMAB, RB); 1815 (BHCB, HAMAB, RB); Vila do Trem, 5 Jul 2008 (fl,fr), *L.A. Pereira et al. 1822* (BHCB, HAMAB, RB); Santana, Ilha de Santana, 12 Jul 2008 (fl,fr), *L.A. Pereira et. al. 1840, 1841, 1842* (HAMAB, HB, RB); 19 Jul 2008 (fr) *L.A. Pereira et al. 1867* (HAMAB, HB, RB); Vila do Trem, 5 Jul 2008 (fl,fr), *L.A. Pereira et al. 1822* (BHCB, HAMAB, RB).

Capsicum baccatum var. **umbilicatum** (Vell.) Hunz. et Barboza, Kurtziana 26:27. 1998. (**Fig. 2B**). *Capsicum umbilicatum* Vell., *Fl. Flum.* 60. (1825) 1829 "Colitur hortis" (non vidi).

Subarbustos hasta 1,50 m alt. Tallos 3–4-costados, glabrescentes. Hojas con láminas ovadas, de 5–12 × 3–4,6 cm, base atenuada y desigual, ápice acuminado, margen ciliado, epifilo glabrescente, hipofilo con densa pubescencia patente a lo largo del nervio medio; pecíolos de 2,8–7,5 cm de largo. Flores 2 ó 3 por nudo reproductivo; pedicelos geniculados apicalmente, péndulos, ca. 2 mm de largo, glabros. Cáliz de 2,3 mm de largo, con 5 dientes subapicales breves, cubiertos por pelos muy cortos. Corola blanca con dos manchas amarillas o verdosas difusas en la base de cada lóbulo y parte del limbo. Estambres 5, anteras amarillas. Gineceo con heteromorfismo estilar; ovario 3–4-carpelar. Bayas péndulas, umbonado-umbilicadas, 3–4 × 3,7–4,9 cm, de color rojo-anaranjadas. Semillas discoidales, comprimidas, de color amarillo pálido, de 3,5–4,2 × 3,1–3,5 mm, episperma finamente reticulado.

Distribución geográfica.—No se encuentra al estado silvestre sino domesticada y cultivada en diversas regiones. Hasta ahora se la ha reportado en Estados Unidos, México, Perú, Bolivia, Brasil y Argentina (Hunziker & Barboza 1998).

Para las comunidades indígenas de Roraima, es conocida como "chapéu-de-frade," "cabeça-de-frade," "chapéu-de-bispo," "pimenta-chapéu," "pimenta-de-flor" y "pimenta-de-cheiro" (sub nom. *C. baccatum* var. *pendulum*, Barbosa et al. 2006). En la única localidad del APA del Río Curiaú (Tabla 2) donde se registró esta variedad, se la denomina "pimenta-de-cheiro-amarela" y se usa sólo como condimento. Es llamativo que los quilombolas de este lugar solo reconozcan una única etnoespecie aludiendo a los frutos, sobre todo a su sabor ("cheiro": palabra que se usa para el sabor característico de *C. chinense*) y color ("amarela" por amarillo, color un poco antes de llegar a la madurez) más que a su forma. En *Capsicum baccatum* var. *umbilicatum*, la forma de los frutos es bastante constante; las bayas son característicamente umbonado-umbilicadas, lo que da la apariencia de un "sombrero," de allí los nombres registrados por los indígenas de Roraima (Barbosa et al. 2006).

Material estudiado: **BRASIL. Amapá:** Macapá, Minipolo Hortifruti da Fazendinha, 5 Aug 2008 (fl,fr) *L.A. Pereira et al. 1824* (HAMAB, RB); Vila do Trem, Rod. BR 156 km 10, 8 Jul 2008 (fl,fr), *L.A. Pereira et al. 1830* (HAMAB, RB).

Capsicum chinense Jacq., Hort. Bot. Vindob. 3:38, t. 67. 1776. (**Fig. 4A–C**).

Subarbustos o arbusto hasta de 2,5 m alt. Tallos superiores aristados, glabros a glabrescentes. Hojas verde oscuras, membranáceas, láminas ovado-elípticas, de (4–)5–7 × 3–4,2 cm, base cuneada, ápice acuminado; epifilo e hipofilo glabrescentes; pecíolos de 1,5–2 cm de largo. Flores 2 o más por nudo reproductivo, pedicelos no geniculados, péndulos, glabros. Cáliz de 2,2–2,4 mm de largo, con 5 dientes subapicales diminutos, cubiertos por pelos muy cortos. Corola cremosa, de 6,5–8 mm de largo, con 5–6 lóbulos glabros por fuera y muy papilosos en los márgenes. Estambres 5–6, anteras blanca-verdosas o violáceas; ovario subgloboso,

3,5 mm × 3,5 mm, estilo a la misma altura de los estambres, 3,8–4,1 mm de largo. Bayas péndulas, ovadas o subobovadas, 1,5–4 × 1–3 cm, de color rojo-anaranjadas o amarillas; cáliz fructífero con constricción basal bien evidente. Semillas amarillentas, episperma finamente foveolado.

Distribución geográfica.—*Capsicum chinense* se cultiva en diversas partes del mundo. En Brasil, es la especie más domesticada por los indígenas (Tabla 2); se encuentra en las regiones centro-oeste y nordeste pero el centro de mayor diversidad es la cuenca de la Amazonía (Bosland & Votava 2000; Carvalho & Bianchetti 2008).

Al igual que en otras regiones de Brasil, presenta una gran variedad de etnoespecies en el área de estudio. Sus nombres suelen variar según el color, sabor, forma, picor y olor del fruto, entre otros. Es reconocida localmente con los mas variados nombres: "pimenta-amarela-ardosa," "pimenta-amarela-de-cheiro," "pimenta camapú," "pimenta-de-cheiro," "pimenta-de-cheiro- tacacá," "pimenta-de-cheiro-de-panela" y "pimenta-de--cheiro-redondinha-ardosa" (Tabla 1).

En ausencia de la "pimenta malagueta" (*C. frutescens*), en el APA del Rio Curiaú y, principalmente en otras localidades de estado del Amapá, la población local utiliza esta especie para desobstrucción de furúnculos, antiespasmódico y para alejar el "mal de ojo," especialmente las variedades con frutos de color rojo. En Amapá es llamada "pimenta de cheiro" y, a menudo, en otras regiones de Brasil es denominada "pimenta de bode," "pimenta de cheiro," "cumari do pará," "murupi," "habanero," "biquinho," entre otros.

Material estudiado: **BRASIL. Amapá:** Macapá, APA da Fazendinha, 26 May 2009 (fr), *L. Espindola-Nascimento & L.S. Simoa 05, 06* (HAMAB, RB); (fl), *L. Espindola-Nascimento & L.S. Simoa 04* (HAMAB, RB); 28 May 2009 (fl), *L. Espindola-Nascimento & J.R.Pinheiro 13* (HAMAB, RB); APA do rio Curiaú, Comunidade Curiaú de Dentro, 2 May 2008 (fl,fr), *L.A. Pereira et al. 1699* (HAMAB); Comunidade Curiaú de Fora, 14 Jul 2008 (fr), *L.A. Pereira & W.M.S.Severino 1854* (HAMAB, RB); Distrito de Fazendinha, Horto do IEPA, 20 Jul 2008 (fl,fr), *L.A. Pereira 1873* (HAMAB, HB, RB); Pólo Hortifruti, 8 Nov 2008 (fl,fr), *L.A. Pereira 1902* (BHCB, HAMAB, RB); 8 Nov 2008 (fl,fr), *L.A. Pereira 1904* (BHCB, HAMAB, RB); 8 Nov 2008 (fl,fr), *L.A. Pereira 1905* (BHCB, HAMAB, RB); 8 Nov 2008 (fr), *L.A. Pereira 1906* (BHCB, HAMAB, RB); 8 Nov 2008 (fl,fr), *L.A. Pereira 1908* (BHCB, HAMAB, RB); Linha D, Rodovia AP 20, Km 8, 8 Jul 2008 (fl,fr), *L.A. Pereira 1834* (HAMAB, RB); 5 Jul 2008 (fl,fr), *L.A. Pereira 1816* (HAMAB, RB); 8 Jul 2008 (fr), *L.A. Pereira 1837* (HAMAB, RB); Minipólo Hortifruti da Fazendinha, 5 Jul 2008 (fl,fr), *L.A. Pereira 1817* (HAMAB, RB); 5 Jul 2008 (fl,fr), *L.A. Pereira et al. 1816* (HAMAB, RB); 5 Jul 2008 (fl,fr), *L.A. Pereira et al. 1821* (HAMAB, RB); Vila Ressaca, Rod. do Curiaú, 14 Jul 2008 (fr), *L.A. Pereira 1851, 1852* (HAMAB, RB); Vila do Trem, Rod. BR 156, Km 10, 8 Jul 2008 (fl,fr), *L.A. Pereira et al. 1827, 1828,* (HAMAB, RB); 8 Jul 2008 (fl,fr), *L.A. Pereira et al. 1831* (HAMAB, HB, RB); 8 Jul 2008 (fl), *L.A. Pereira 1833* (HAMAB, RB); 10 Nov 2008 (fl), *L.A. Pereira et al. 1918* (BHCB, HAMAB, RB); 10 Nov 2008 (fr), *L.A. Pereira et al. 1920* (BHCB, HAMAB, RB); Santana, Ilha de Santana, 12 Jul 2008 (fl,fr) *L.A. Pereira et al. 1846* (HAMAB, HB, RB); 12 Jul 2008 (fl,fr) *L.A. Pereira et al. 1839* (CEPEC, HAMAB, HB, RB); 19 Jul 2008 (fl,fr) *L.A. Pereira et al. 1864* (HAMAB, RB); 19 Jul 2008 (fr) *L.A. Pereira et al. 1868* (HAMAB, HB, RB); 19 Jul 2008 (fr) *L.A. Pereira et al. 1870* (HAMAB); 8 Nov 2008 (fr) *L.A. Pereira et al. 1901* (BHCB, HAMAB, RB).

Capsicum frutescens L., Sp. Pl. 1:189. 1753. (**Fig. 4D–G**).
Subarbustos o arbustos hasta de 2,5 m alt. Tallos ligeramente aristados, glabrescentes. Hojas verde oscuras, papiráceo-membranáceas, brillantes, láminas oblongo-elípticas u ovado-elípticas, 8–12,5 cm long. × 4–6 cm lat., base asimétrica, ápice agudo, epifilo e hipofilo glabros; pecíolos de 0,5–1 cm. Flores 1 ó 2 por nudo reproductivo, pedicelos geniculados, erectos, glabros, de 1–2,3 cm. Cáliz de 2,5 mm long., glabrescente, con 5 dientes subapicales cortos. Corola cremosa o amarillo-verdosa, ca. 6,5 mm de largo, lóbulos glabros por fuera y con papilas en los márgenes. Estambres 5, filamentos 1,2 mm, anteras blancas o azuladas. Gineceo sin heteromorfismo estilar; ovario oblongo-ovoide, 4 × 1,8 mm, estilo 5 mm de largo, supera la longitud de los estambres. Bayas erectas, rojo-anaranjadas, elipsoides, ovoides u oblongo-ovoides; cáliz fructífero cupuliforme, sin constricción basal evidente o ausente, 1,5–4 cm de largo. **Semillas** amarillentas, episperma finamente foveolado.

Distribución geográfica.—En Brasil es más frecuente en la región Norte, aunque es ampliamente utilizada en las regiones Nordeste y Sudeste (Carvalho & Bianchetti 2008). Se distribuye desde Centro América, Antillas y Caribe hasta las tierras bajas del Sudeste brasileño. Crece en todos los entornos de la APARC principalmente debido a la dispersión realizada por los pájaros (Tewksburry & Nabhan 2001); siempre existe una planta de pimienta en las quintas, cultivos, campos y capoeiras. Es considerada, una de las especies de pimientas más domesticadas en Brasil junto a *C. chinense*.

Se reconocen en el estado del Amapá tres etnoespecies que se usan como planta medicinal, ritualística, alimenticia, repelente de insectos, entre otras (Tabla 2): "pimenta malagueta" (fruto ca. 2,5 cm de largo), es la más difundida y ampliamente usada en la comunidad, "pimenta malaguetão" (fruto ca. 4,5–5 cm de largo) y "pimenta malaguetinha" (fruto ca. 1,5 cm de largo). Estas etnoespecies son citadas por todos los especialistas entrevistados en las distintas localidades estudiadas.

Los quilombolas utilizan la hojas de "pimenta malagueta" para el tratamiento de enfermedades, especialmente de la piel ("pano branco" y "forúnculo"), contra el reumatismo, dolores de garganta y dientes, y, según declaraciones de los encuestados son plantas mágico-simbólicas, con poder para evitar el "*mal de ojo*," curar la "*panemeira*" y dar "*buena suerte en todo*" (Pereira et al. 2007).

A diferencia de lo que señalado para las comunidades indígenas de Roraima (Barbosa et al. 2006), donde se registró un cultivar de *C. frutescens* ("malagueta doce") con bajo tenor de pungencia, en la comunidad de Curiaú las tres etnoespecies reconocidas son muy picantes.

Material estudiado: **BRASIL. Amapá:** Macapá, Linha D, Rod. AP 20 km 8, 8 Jul 2008 (fr), *L.A. Pereira et al. 1836* (HAMAB, RB); Vila do Trem, Rod. BR 156 km 10, 8 Jul 2008 (fl,fr), *L.A. Pereira et al. 1829* (HAMAB, RB); Rod. BR. 156 km 10, 8 Jul 2008 (fl,fr), *L.A. Pereira et al. 1826* (HAMAB, RB); APA do Rio Curiaú, Comunidade Curiaú de Fora, 14 Jul 2008 (fl,fr), *L.A. Pereira & W.M.S.Severino 1885* (HAMAB, HB, RB); 7 May 2008 (fl,fr), *L.A. Pereira et al. 1808* (HAMAB, RB); Santana, Ilha de Santana, comunidade Ilha de Santana, 19 Jul 2008 (fl,fr), *L.A. Pereira et al. 1865* (HAMAB, RB).

CONSIDERACIONES FINALES

A través de este estudio se pone en evidencia que la comunidad afro-descendiente de Curiaú ha recurrido a las reservas florísticas autóctonas de la región incorporándolas tanto en su alimentación como en su sistema de salud como recursos medicinales.

La comunidad de quilombolas del Curiaú ha demostrado una significativa acumulación de conocimientos sobre los distintos usos de las "pimientas" (*Piper* spp. y *Capsicum* spp.), sobre todo en lo que se refiere a alimentos y usos medicinales. En menor medida, y en el caso de las etnoespecies de *Capscium*, se menciona por primera vez su uso como plantas simbólicas, para curar "males" o dar "buena suerte."

La comunidad emplea más las especies de *Capsicum* que de *Piper*. En el pasado, los quilombolas cultivaban *Piper nigrum* ("pimenta-do-reino"); hoy en día este cultivo ha disminuido considerablemente al punto de no haberse encontrado ningún cultivo en las quintas de los especialistas entrevistados; por el contrario, se adquieren las drupas de esta especie en el comercio local para su consumo. Tanto *P. marginatum* como *P. tuberculatum* se usan solamente con fines terapéuticos. En cambio, los 5 taxones de *Capsicum* registrados tienen usos variados y con distintos grados de importancia. *Capsicum chinense* y *C. frutescens* son las especies más empleadas por la comunidad; ambas son consideradas un ingrediente importante en sus comidas (por el sabor y pungencia que confieren los frutos), y se emplean para distintas dolencias físicas. Si bien se emplean los frutos como condimento de las dos variedades de *C. annuum* y de *C. baccatum* var. *umbilicatum*, éstas son plantas que tienen fundamentalmente fines ornamentales y comerciales. Los quilombolas usan solamente las hojas de *Capscium annuum* var. *glabriusculum* como medicinal.

A pesar de las modificaciones adquiridas por la domesticación de diversas especies de "pimientas," las características vegetativas y florales de las especies de *Capsicum* en la comunidad estudiada (tipo de hojas, cáliz, posición de los pedicelos, forma de los ovarios, entre otros) son las que se mantuvieron más constantes. En cambio, la domesticación tendió hacia el mejoramiento de las frutos (particularmente en *C. annuum*, *C. chinense* y *C. frutescens*), modificándose el tamaño, color, pungencia y sabor. Los quilombolas aprendieron a seleccionar la especies más palatable (*C. chinense*), las más picantes (*C. chinense* y *C. frutescens*), la más ornamental (*C. annuum* var. *glabriusculum*), las que más comercializan (*C. frutescens*, *C. chinense* y *C. annuum* var. *annuum*), las de interés medicinal (*C. frutescens* y *P. marginatum*).

El uso de las especie nativas de "pimientas" realizado por la comunidad estudiada ha demostrado ser sustentable para *Piper marginatum* y *P. tuberculatum* que crecen espontáneamente; no obstante, si bien se reporta en el área de estudio su uso limitado como medicinal, consideramos que son dos entidades importantes a ser tenidas en cuenta en la elaboración del plan de gestión de conservación de la APARC.

Con respecto a las "pimientas" de *Capsicum*, los quilombolas tienen incorporadas ciertas prácticas de conservación pues preferieren utilizar alternativamente las plantas cultivadas en sus quintas para reducir el impacto de su recolección en el bosque. A partir del conocimiento obtenido sobre la intensidad del uso de las especies de *Capsicum*, podría ser posible diseñar un plan de manejo en el APARC, dirigido hacia las dos especies más explotadas: *C. chinense* y *C. frutescens.*

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CHROMOSOME NUMBER FOR *ARCYTOPHYLLUM FASCICULATUM* (RUBIACEAE)

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ABSTRACT

A chromosome number of 2*n* = 12 II is reported for *Arcytophyllum fasciculatum* (A. Gray) Terrell & H. Rob. (Rubiaceae), a species known in recent floristic treatments as *Hedyotis intricata* Fosberg. This is the first report for the species, and the second report for a species of *Arcytophyllum*.

RESUMEN

Un número de cromosomas de 2*n* = 12 II se obtuvo para *Arcytophyllum fasciculatum* (A. Gray) Terrell & H. Rob. (Rubiaceae), una especie conocida en obras florísticas recientes como *Hedyotis intricata* Fosberg. Este informe del número cromosomático es el primero para esta especie, y el segundo para una especie del género *Arcytophyllum*.

A meiotic chromosome number of 2*n* = 12 II was obtained from each of two proximally located plants of *Arcytophyllum fasciculatum* (A. Gray) Terrell & H. Rob.: Texas. Brewster Co.: Big Bend National Park, Upper Burro Mesa Trail, 0.43 mi from Ross Maxwell Scenic Drive, 3875 ft., 16 Jul 2010, *A. Leavitt 325, 326* (SRSC). Buds were fixed in modified Carnoy's Solution (4:3:1). Meiotic observations followed the use of standard squash techniques and acetocarmine stain. Interpretation of meiotic configurations was complicated by 1) small cell size, 2) consistently "clumped" chromosomes at metaphase I, anaphase I, and in meiosis II, and 3) heteromorphic chromosomes (Fig. 1). Bivalents were dark-stained and often clearly differentiated at diakinesis, prophase I; hundreds of chromosomal spreads were observed at this stage. Diakinetic configurations were interpreted as consisting of 12 II, approximately (if not exactly) half of them larger "ring" bivalents and half of them smaller "rod" bivalents.

Based on morphological considerations, Terrell and Robinson (2010) transferred *Hedyotis intricata* Fosberg, a species of northern Mexico, Trans-Pecos Texas, and southern New Mexico, to *Arcytophyllum* Willd. ex Schult. & Schult. f., a genus of 15 primarily Andean species (Mena 1990), concluding that *A. fasciculatum* (= *H. intricata*) is most closely related to *A. thymifolium* (Ruiz & Pavon) Standl. of Columbia, Ecuador, and Peru. Apparently the only species of *Arcytophyllum* for which chromosome numbers have been reported previously is *A. thymifolium*; 2*n* = ca. 30 and 2*n* = 36 (Federov 1969). Chromosome numbers have been useful in evaluating relationships in tribe Spermacoceae (Groeninckx et al. 2009), which includes *Arcytophyllum, Hedyotis* L., *Houstonia* L., *Oldenlandia* L., and segregate genera, and involves the aneuploid series *x* = 6, 7, 8, 9, 10, 11, 13, and 17 as reviewed by (Lewis 1962; Terrell 1991; 2001; Terrell et al. 1986; Church 2003). The *n* = 12 reported here, previously missing from the series, is relevant in future phylogenetic considerations in tribe Spermacoceae. Furthermore, the heteromorphic karyotype of *A. fasciculatum* suggests that chromosome morphology might also provide important phylogenetic information in the lineage concerned.

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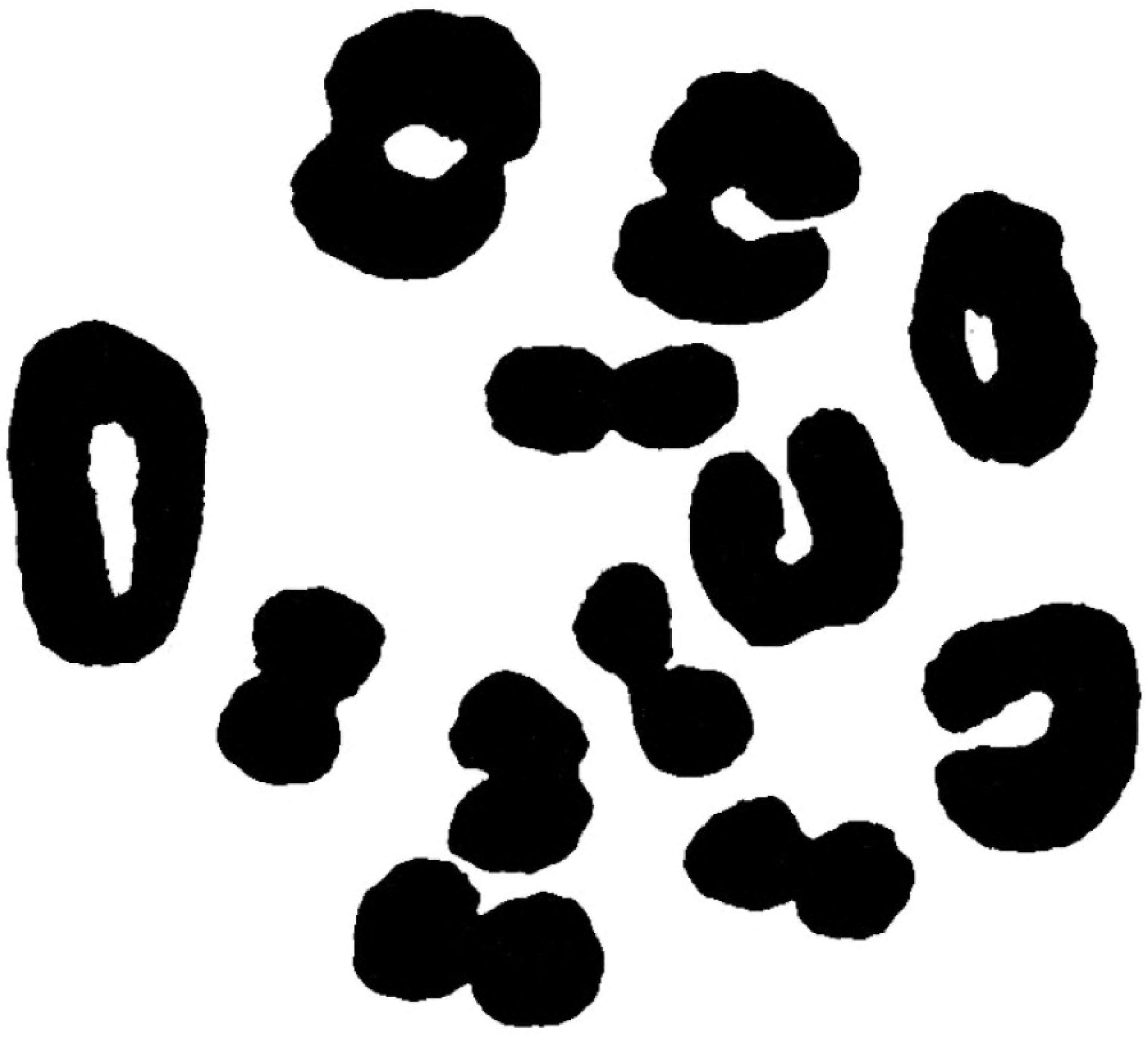

Fig. 1. Free hand drawing, meiotic chromosomes of *Arcytophyllum fasciculatum* (*Leavitt 325*): prophase I, diakinesis; interpreted as 2*n* = 12 heteromorphic bivalents.

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FLORA ENDÉMICA DE NUEVO LEÓN, MÉXICO Y ESTADOS COLINDANTES

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RESUMEN

El objetivo del presente trabajo es conocer las especies endémicas al estado de Nuevo León y sus estados colindantes. A través de una revisión bibliográfica, consulta de bases de datos y trabajo de campo se integró una lista de plantas endémicas estatales y regionales que incluye información de los municipios en los que se distribuyen, su hábitat y sinonimias. Se contabilizan un total de cinco géneros y 159 especies endémicas a Nuevo León, esto representa alrededor del 5% del total de la flora estatal. Al extender los limites geográficos al los estados colindantes, el número de especies aumenta a 191. El municipio de Galeana en la Sierra Madre Oriental presenta más del 50% de las especies endémicas estatales, solo 13 especies con distribución restringida al estado se incluyen en la NOM-059-SEMARNAT-2001. Los ecosistemas con mayor diversidad de endemismos son los bosques en sus diversas asociaciones y la vegetación gipsófila.

Palabras Clave: flora, endemismo, México, biodiversidad

ABSTRACT

The main objective of this work is to know the endemic flora of the state of Nuevo Leon and neighboring states in northeast Mexico. Through bibliographic research, database consulting, and field work, a list of endemic vascular plants was compiled with information about nomenclatural synonyms, habitat, and municipalities in which the species occur. A total of 5 genera and 159 species were found to be endemic in Nuevo Leon representing 5% of the state's flora. By extending the geographic range to the neighboring states, a total of 191 species are accounted as regional endemics. Galeana municipality in the Eastern Sierra Madre, harbors more than 50% of the state endemics; only 13 state endemic species are listed under a federal protection category on NOM-059-SEMARNAT-2001. Ecosystems with the most endemic diversity are forest and gypsophylus vegetation.

Key Words: flora, endemic, Mexico, biodiversity

México es un país megadiverso, se estima que ocupa el 4° lugar mundial en riqueza florística (Mittermeier et al. 1997; Villaseñor 2003), la cual incluye casi 23,000 especies de plantas vasculares, con un endemismo del 52% (Rzedowski 1998). Esta diversidad esta distribuida en 2,804 géneros (7.8% endémicos) y 304 familias (Villaseñor 2004), y se atribuye a factores físicos como la orografía, climas, hidrología y la ubicación del pais entre los reinos biogeográficos neartico y neotropical (Rzedowski 1978).

A pesar de que México cuenta con más de 2.3 millones de colectas botánicas y existen numerosas floras regionales, aún no se cuenta con una flora nacional y se estima que un 30% del territorio aún no está incluido en algún estudio florístico formal (Sosa y Dávila 1994). La necesidad de documentar la flora es fundamental para respaldar numerosas investigaciones biológicas, tanto básicas como aplicadas (Vázquez-García et al. 2004).

En cuanto a la diversidad del estado de Nuevo León se tiene el antecedente de un listado florístico elaborado por Rojas-Mendoza (1965), el cual incluye 148 familias de plantas vasculares, con un total de 1,484 especies o categorías subespecíficas en 657 géneros; esta lista florística se incrementó a 3,175 especies, 1,031 géneros y 158 familias de plantas vasculares (Villarreal y Estrada 2008), mientras que otras estimaciones señalan un total de 2,903 especies de plantas vasculares distribuidas en 157 familias y 910 géneros, además de 360 taxa infraespecíficos, registrándose 110 especies endémicas para el estado (Velazco 2009).

El estudio de especies endémicas o consideradas como prioritarias para su conservación presenta avances en estados como Coahuila donde se estima existen 190 especies en esa categoría (Villarreal y Encina

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2005), mientras que en Tamaulipas se listan 97 especies raras, amenazas y en peligro de extinción donde además son señaladas 8 especies endémicas estatales (Malda 1990); por otra parte, en el estado de Texas en los Estados Unidos de América se listan más de 300 especies endémicas (Poole et al. 2007); para Nuevo León se estimaron 200 especies endémicas a la región centro – sur del estado, en la zona colindante con el estado de Coahuila, sin especificar cuales son dichas especies (Hinton y Hinton 1995); existen también antecedentes relativos a las especies listadas en la NOM-059-SEMARNAT-2001 (Alanís et al. 2004); por otra parte, a pesar de que aun existen omisiones para los estados de Zacatecas y San Luís Potosí, con la ayuda de los trabajos seriados para el conocimiento de la flora de Veracruz (Castillo 2010), la región del bajío y regiones adyacentes (Rzedowski y Calderón 2010), así como la flora del valle de Tehuacán – Cuicatlán (Novelo 2010) seguramente se terminaran por subsanar estos vacíos.

Tomando en cuenta que la generación de inventarios biológicos es la base para un manejo apropiado de los recursos naturales, así como para la conservación de los mismos (Vovides et al. 1997), el presente trabajo tiene por objeto el presentar una lista base de especies endémicas o con distribución restringida al estado de Nuevo León y estados colindantes que deben ser consideradas como prioridad en su estudio y conservación no solo en Nuevo León, sino, en el noreste de México y en algunos casos el sur de Estados Unidos (Texas), además de servir como una herramienta para la toma de decisiones a nivel gubernamental para el desarrollo y la planeación del desarrollo urbano y económco.

MATERIALES Y MÉTODOS

Área de estudio: Nuevo León, México

Localización

El estado de Nuevo León se encuentra localizado en el noreste de la República Mexicana (Fig. 1); colinda hacia el norte con los Estados Unidos de América, al noroeste y oeste con los estados de Coahuila y Zacatecas, al sur y sureste con el estado de San Luis Potosí, y al noreste y sureste con el estado de Tamaulipas. Tiene una extensión cercana a los 65,000 Km^2, ocupando el decimotercer lugar en el país por su extensión. Se encuentra ubicado entre los paralelos 23°10'27" y 27°46'06" de latitud norte y los meridianos 98°26'24" y 101°13'55" de longitud oeste. Es cruzado en el sur por el Trópico de Cáncer en el municipio de Mier y Noriega en el paralelo 23°27'. Cabe mencionar que por su latitud, está situado en parte dentro del cinturón de los grandes desiertos del mundo.

Provincias florísticas

En el estado se presentan tres zonas florísticas bien definidas (Rzedowski y Reyna 1990) las cuales corresponden a las descritas en algunos casos como provincias fisiográficas (Alanís 1996):

Planicie Costera del Golfo: ocupa la porción norte, noreste y centro del estado, se presentan elevaciones desde los 50 a los 250 msnm, su topografía es de forma general plana, a excepción de algunos cerros y lomeríos de poca altitud, es en esta zona donde se localizan los principales ríos del estado, los cuales fluyen hacia el este en dirección al Golfo de México. Geológicamente hablando esta región se constituye por sedimentos de la era Cenozoica del periodo Terciario

Sierra Madre Oriental: esta zona cruza el estado de sureste al noroeste, con algunas secciones que pueden considerarse islas geográficas, como es el caso de la Sierra Picachos y la Sierra Papagayos. Está compuesta de terrenos muy accidentados que forman pliegues paralelos y que alcanzan un promedio de 2,000 msnm, es en esta provincia donde se localizan los picos más altos, entre los cuales están el Cerro El Potosí, La Ascensión y San Antonio Peña Nevada todos con cerca de 4,000 msnm.

Altiplano Mexicano: está localizada en la sección sur suroeste del estado, esta compuesta de terrenos planos y algunas elevaciones montañosas aisladas y lomerios suaves, su altura varía entre los 1,500 y 2,000 msnm.

Geología

Nuevo León es un estado compuesto mayormente por rocas sedimentarias, con excepción de unas cuantas zonas con rocas metamórficas e ígneas intrusivas localizadas puntualmente en ciertos municipios del

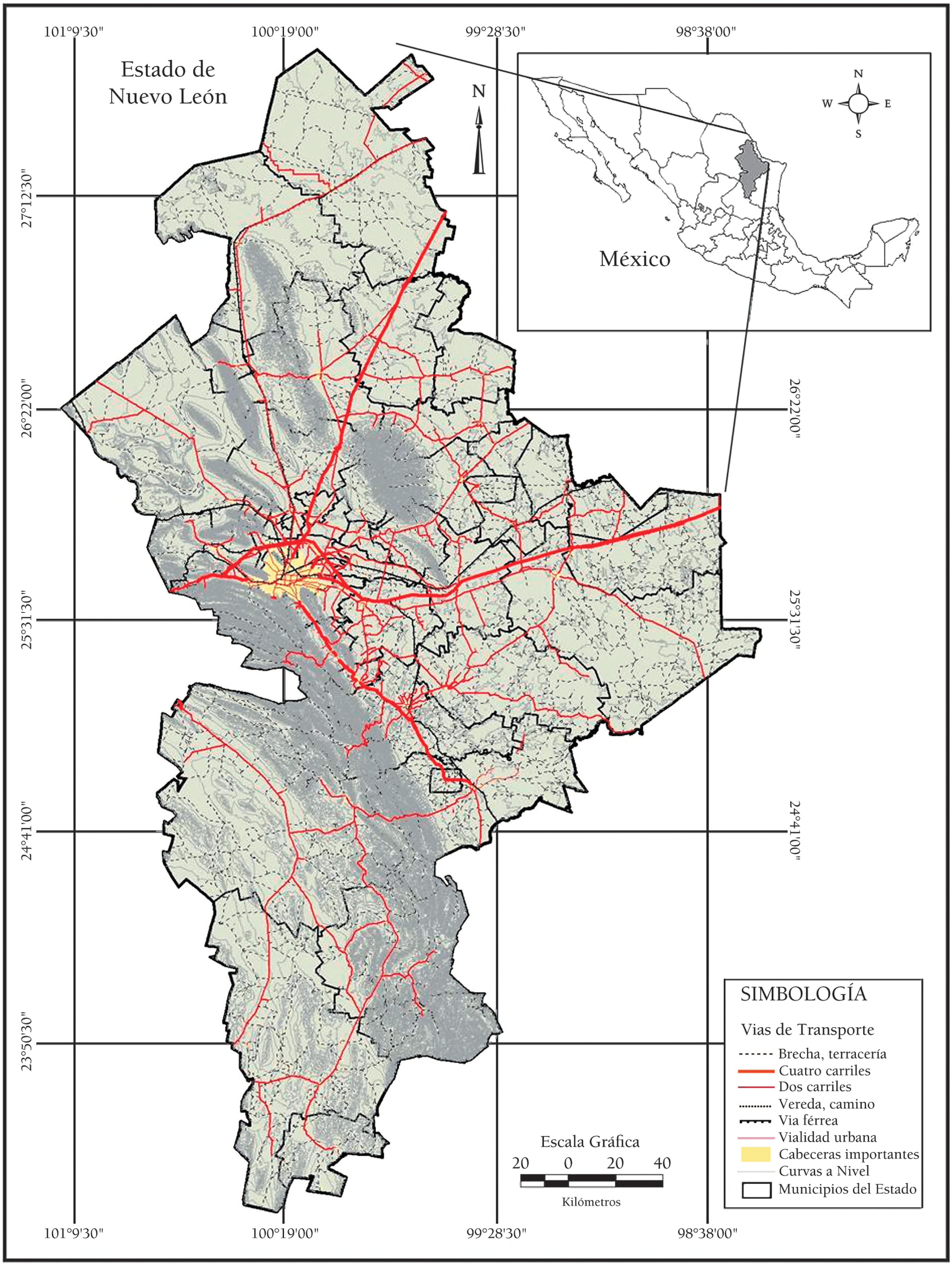

Fig. 1. Ubicación del estado de Nuevo León en el noreste de México.

estado como la Sierra Picachos en Sabinas Hidalgo en el centro norte del estado; el resto se originó a partir de los sedimentos acumulados en el fondo de los mares primitivos los cuales dieron origen a las rocas caliza, lutitas y areniscas, donde las rocas calizas se presentan casi de manera única en la Sierra Madre Oriental, y se combinan de manera esporádica con lutitas y areniscas; mientras que en la Planicie Costera del Golfo se presentan zonas de origen aluvial, así como lutitas y areniscas, las cuales se mezclan en diversos grados formando conglomerados. En el Altiplano Mexicano se presentan en su mayor parte zonas de origen aluvial y en menor grado rocas calizas y lutitas y areniscas, es en esta zona donde se presentan además sitios de origen lacustre en el municipio de Galeana, las cuales ocurren de manera aislada en otros municipios en el norte del estado como Anahuac. Vale la pena destacar que en el sur del estado en la confluencia de la Sierra Madre Oriental y el Altiplano Mexicano se presentan zonas gypsófilas las cuales son de gran importancia desde el punto de vista florístico. Las rocas más antiguas son algunos esquistos de la era precámbrica en el municipio de Aramberri; por otra parte la Sierra Madre Oriental es de origen Jurásico y Cretácico de la era mesozoica, mientras que la Planicie Costera del Golfo se origina de manera más reciente en el terciario de la era cenozoica (Instituto Nacional de Estadística, Geografía e Informática 1986).

Climatología

En el estado predominan los climas tipo B caliente y seco de la clasificación de Köppen, Bw árido o muy seco, y Bs semiárido o seco. También se presentan otros tipos de climas, los cuales tienen una menor ocurrencia o dominancia, entre estos podemos mencionar el semicálido (A)C y el templado subhúmedo C(W). Mientras que en zonas con altitudes arriba de los 3,000 msnm en la Sierra Madre Oriental se pueden observar climas tipo alpino y subalpino de manera muy restringida como es el caso de San Antonio Peña Nevada y el Cerro del Potosí en los municipios de General Zaragoza y Galeana respectivamente. (Instituto Nacional de Estadística, Geografía e Informática 1986). El régimen de precipitación pluvial muestra una gran variación, en las zonas más secas, localizadas la Planicie Costera del Golfo, en los municipios de García, Mina y Bustamante y el Altiplano mexicano en los municipios de Galeana, Doctor Arroyo, Aramberri, Mier y Noriega y algunas zonas de General Zaragoza, la precipitación puede llegar a ser menor a los 200 mm anuales; en contraste, la zona con mayor precipitación y humedad se localiza en la vertiente este de la Sierra Madre Oriental, al sureste de la ciudad de Monterrey, en los municipios de Cadereyta Jiménez, Juárez, Santiago, Allende y Montemorelos con valores de entre 600 y 900 mm anuales, donde destacan especialmente zonas como la Sierra Cerro de la Silla y el cañón El Calabozo, los cuales están prácticamente inmersos en la zona metropolitana de Monterrey. De manera esporádica se presentan eventos tales como huracanes o tornados, mientras que heladas, granizadas y nevadas se restringen casi de manera exclusiva a la Sierra Madre Oriental y afectan zonas muy restringidas en esta zona (Instituto Nacional de Estadística, Geografía e Informática 1986).

Hidrología

Se presentan dos cuencas principales en lo que se refiere a la hidrología superficial, una localizada al Norte denominada Cuenca del Río Bravo y otra al sur también conocida como Cuenca del Golfo de México. Dentro de estas, se presentan cuatro cuencas: Bravo – Conchos (RH24), San Fernando – Soto La Marina (RH 25), Pánuco (RH 26) y El Saldao (RH 37), las cuales a su ves se dividen en 14 subcuencas. A continuación se enlistan los principales ríos del Estado:

Río Salado—Río Sabinas—Río San Juan—Río Pilón—Río Pesquería—Río Conchos—Río Blanco—(Instituto Nacional de Estadística, Geografía e Informática 1986).

Edafología

Debido a la naturaleza mayormente sedimentaria del estado y a la predominancia de rocas como las calizas y lutitas, los suelos presentan una marcada tendencia arcillosa y calcárea, su principal forma de origen es la aluvial, es decir, por arrestare de materiales por agua. Se reconocen algunas zonas muy localizadas donde los suelos se han originado por intemperismo de rocas ígneas, como es el caso de la Sierra Picachos en los municipios de Sabinas Hidalgo y Agualeguas (Instituto Nacional de Estadística, Geografía e Informática 1986). De acuerdo a la clasificación internacional, los suelos que predominan en Nuevo León, son los

litosoles, presentes en gran medida en la Sierra Madre Oriental mezclado en ciertas zonas con rendzinas, por otra parte se presenta una mayor diversidad de suelos en la Planicie Costera del Golfo y el Altiplano Mexicano entre los que destacan los castaños o chesnut, los de desierto y semidesierto, grises o xerozem y suelos negros o chernozem.

Vegetación

Se anexa un resumen descriptivo de la vegetación del estado el cual se integra a partir de la información consultada en Miranda y Hernández (1963), Rojas Mendoza (1965), Rzedowski (1978) y Alanis Flores (1996).

Bosque de Pino.—La distribución de estos bosques puede ocurrir en lugares templados y húmedos, con el factor térmico decreciente a medida que se asciende en altitud; se ubica a partir de 900 y 1,000 msnm. Se trata de una comunidad con árboles hasta 22 m de alto. Se localizan en los municipios de Santa Catarina, Monterrey, San Pedro Garza García, Santiago, Montemorelos, Allende, Linares, Rayones, Iturbide, Galeana, Aramberri y Zaragoza; están asociados comúnmente con algunas especies de encinos (*Quercus* spp.) y madroño (*Arbutus xalapensis*).

Las especies de pinos características son pino ocote (*Pinus teocote*), pino blanco (*P. pseudostrobus*), pino real (*P. arizonica*), pino ayacahuite (*P. ayacahuite*), y pino negro (*P. hartwegii*). Podemos encontrar variantes de estos bosques como son los de pino piñonero (*P. cembroides*), que se localizan en los municipios de San Pedro Garza García, Santiago, Montemorelos, Rayones y Galeana; asimismo en áreas muy restringidas en la parte norte de Nuevo León en la Sierra de Lampazos. Prosperan en áreas de baja precipitación entre los 2,000 a 2,600 msnm, sobre suelos someros y rocosos. Este tipo de bosque presenta espacios abiertos de árboles bajos de 4 a 8 m de altura, con copas redondeadas y troncos con diámetros de 30 a 40 cm a la altura del pecho. Las principales especies arbóreas del bosque de pino piñonero de Galeana son (*P. cembroides*), pino garabatillo (*P. greggii*), enebros (*Juniperus flaccida* y *J. deppeana*) y madroño (*Arbutus xalapensis*). Se localiza también en áreas limítrofes del matorral desértico del altiplano y con frecuencia se asocian especies como la palma samandoca (*Yucca carnerosana*), palma china (*Yucca filifera*), magueyes (*Agave* spp.) y arbustos diversos.

Desde los 3000 metros de altitud hasta la cima del cerro El Potosí en Galeana, se localiza un tipo especial de vegetación en forma de matorral, ramificados desde la base del tallo, de menos de 2 m de altura, de pinos enanos (*Pinus culminicola*) que colindando con el prado alpino, forma una franja continua en el declive oriental y sur, presentándose además en dos manchones aislados al suroeste y oeste de la cima. Esta se presenta como una comunidad densa y baja en la que el pino enano es dominante.

Bosque de Coníferas.—Los bosques de hallarín-oyamel (*Pseudotsuga – Abies*) son una variante de los bosques templados que se caracteriza por especies de gran atractivo escénico con árboles de formas típicas piramidales. Este tipo de vegetación está constituido por árboles altos de 15 a 25 m, que se localizan en cañones protegidos con climas fríos y húmedos, generalmente entre 2,000 a 2,500 msnm en los municipios de Galeana, Iturbide, Aramberri y Zaragoza. Las especies que sobresalen dominando en el dosel arbóreo son pino blanco (*Pinus peudostrobus*) y pino ocote (*Pinus teocote*) junto con el hallarín (*Pseudotsuga menziesii* y *flahaulti*), oyamel (*Abies vejarii y A. mexicana*), cedro blanco (*Cupressus arizonica*) y diversas especies de enebros (*Juniperus* spp.).

Hay otro tipo de bosque en áreas restringidas, formando manchones más o menos puros en algunas pequeñas áreas, de bosques de cedro (*Cupressus* spp.) en Iturbide, Galeana y General Zaragoza. Los árboles no son corpulentos y alcanzan entre 10 y 15 m de altura, las especies características son cedros blancos (*Cupressus arizonica*).

Otra comunidad es la de bosque de enebros (*Juniperus* spp.), que se asocia a los bosques de pinos y encinos. Su forma de vida es arbórea o arbustiva según sean las condiciones ambientales, prosperan en lugares de suelos rocosos de calizas expuestas y baja humedad y su crecimiento es lento. Las especies más comunes son *Juniperus monosperma* y *Juniperus flaccida*. Se encuentran prácticamente a lo largo de toda la Sierra Madre Oriental.

Bosque de Pino – Encino.—Esta unidad se integra por especies de hoja ancha y en agujas, sobre áreas tem-

pladas a subhúmedas en los municipios de Monterrey, Santiago, Allende, Montemorelos, Rayones, Iturbide, Linares, Aramberri, Zaragoza, García, San Pedro Garza García, Bustamante, Mina y Salinas Victoria, A pesar de la amplia gama de condiciones climáticas en la región, la presencia de este tipo de bosque obedece más al factor térmico que a la humedad. Este bosque se presenta entre una altitud de 550 a 900 m. Dominan principalmente los encinos entre los que destacan el encino de asta (*Quercus rysophylla*), encino blanco (*Quercus laeta*), el encino roble (*Quercus polymorpha*) y el encino duraznillo (*Quercus canbyi*) y conviviendo con los encinos se encuentran el pino colorado (*Pinus teocote*) y el pino blanco (*Pinus pseudostrobus*. Los árboles en general no presentan grandes tallas en diámetro o en altura, siendo estas de 10 a 30 cm, y 10 a 14 m respectivamente.

Bosque de encino.—Este tipo de bosques forma parte de la comunidad forestal templada sobre el área de la Sierra Madre Oriental; se pueden localizar en los municipios de Lampazos, Sabinas, Villaldama, Hidalgo, Monterrey, San Pedro Garza García Santiago, Allende, Montemorelos, Rayones, Galeana, Iturbide, Linares, Aramberri y Zaragoza; desde áreas con suelos delgados y rocosos, hasta en sitios de suelos profundos y bien drenados; fisonómicamente se componen de árboles y arbustos que van de 12 a 15 metros de altura, dominando las especies del género *Quercus;* los encinares están muy ligados ecológica y florísticamente con los bosques mixtos y bosques de pinos. Las especies características son encino de asta (*Quercus rysophylla*), encino blanco (*Quercus laeta*), encino roble (*Quercus polymorpha*), encino memelito (*Quercus laceyi*), encino duraznillo (*Quercus canbyi*), encino chaparro (*Quercus pungens*), encino olivo (*Quercus vaseyana*) y encino enano (*Quercus intricada*).

Matorral Submontano.—Es una formación arbustiva y subarbórea muy rica en formas de vida. El vigor, talla y distribución de las especies dominantes y codominantes dependen de la disponibilidad de agua en el suelo y subsuelo. Las formas biológicas dominantes son arbustos o árboles de 4 a 6 metros de alto, con hojas pequeñas, caducifolias y subespinosas. Se ubican en los taludes inferiores de las montañas de hecho forman un extenso umbral que separa los elementos del matorral desértico de las planicies y los bosques de encino y encino-pino existentes en los taludes superiores de a Sierra Madre Oriental. Aunque tiene variantes morfológicas y ecológicas, en términos generales en este matorral las especies más representativas son barreta (*Helietta parvifolia*), anacahuita (*Cordia boissieri*), frijolillo (*Sophora secundiflora*), falso olivo (*Gochnatia hypoleuca*), corvagallina (*Neopringlea integrifolia*), hoja dorada (*Decatropis bicolor*), escobilla (*Fraxinus greggii*), tenaza (*Pithecellobium pallens*), cenizo (*Leucophyllum frutescens*), chaparro prieto (*Acacia rigidula*), guajillo (*Acacia berlandieri*), huizache (*Acacia farnesiana*), hierba del potro (*Caesalpinia mexicana*), mezquite (*Prosopis glandulosa*), chapote manzano (*Dyospiros virginiana*), chapote prieto (*Dyospiros texana*) y palo verde (*Cercidium macrum*). En algunas áreas con hábitats protegidos con abundante humedad y suelos profundos, podemos encontrar agrupaciones pequeñas de encino molino (*Quercus virginiana*). El matorral submontano se localiza en Santa Catarina, San Pedro Garza García, Monterrey, Guadalupe, Santiago, Juárez, Cadereyta, Allende, Montemorelos Rayones, Linares, Lampazos, Villaldama, Hidalgo, El Carmen, Abasolo, Marín e Higueras.

Matorral Espinoso y Mezquital.—Las comunidades vegetales naturales del matorral espinoso y los mezquitales presentan variantes fisonómicas, las especies pueden ser altas espinosas o medianas subinermes, y representan las comunidades vegetales típicas de la región de la Planicie Costera del Golfo. En condiciones de suelo y humedad favorables, los tallos poseen fustes bien definidos y se presentan formas arbóreas de más de 6 metros de altura, entre los que destacan por abundancia y cobertura el mezquite (*Prosopis laevigata*), ébano (*Pithecellobium ebano*), chaparro prieto (*Acacia rigidula*), chaparro amargoso (*Castela texana*), granjeno (*Celtis pallida*), palo verde (*Cercidium macrum*), cruceta (*Randia laetevirens*), anacahuita (*Cordia boissieri*), cenizo (*Leucophyllum frutescens*), guayacan (*Porlieria angustifolia*), tasajillo (*Opuntia leptocaulis*), nopal (*Opuntia engelmannii*), colima (*Zanthoxylum fagara*), y coma (*Bumelia celastrina*), destacando la palma china (*Yucca filifera*) hasta de 10 metros de altura. Este tipo de vegetación se localiza en los municipios de Anáhuac, Lampazos de Naranjo, Sabinas Hidalgo, Vallecillo, Parás, Agualeguas, General Treviño, Doctor Coss, General Bravo, Los Ramones, China, General Terán, Cerralvo, Salinas Victoria, Ciénega de Flores, Higueras, El Carmen,

Abasolo, Salinas Victoria, Los Herreras, Hualahuises, Montemorelos, Cadereyta Jiménez, Allende, Monterrey, Linares, San Nicolás de los Garza, Guadalupe, Juárez, Apodaca, Zuazua, Marín y Rayones.

Matorral Desértico.—Son característicos de los climas áridos y semiáridos del Estado. Su distribución irregular obedece principalmente al patrón de humedad disponible en el suelo. Los suelos de textura arenosa a limo-arenosa y arcillosa, que tienen la capacidad de retener humedad sustentan comunidades densas y cerradas, mientras que los suelos pedregosos que retienen poca agua presentan comunidades vegetales pobres y muy abiertas. Podemos mencionar dos tipos de matorrales desérticos dominantes en Nuevo León.

Matorral Desértico Rosetófilo.—Esta comunidad se presenta sobre flancos montañosos y taludes de varias elevaciones, en los cuales existen afloramientos rocosos o suelos esqueléticos de litosoles. Se localizan en los municipios de Galeana, Rayones, Dr. Arroyo, Aramberri, Zaragoza, Mier y Noriega, García, Santa Catarina, Abasolo, El Carmen, Mina, Lampazos, Bustamante, Salinas Victoria, Villaldama, Higueras, Marín, Dr. González, Cerralvo y Escobedo. Los elementos más conspicuos presentan hojas suculentas agrupadas en rosetas, algunas con espinas terminales o mucrones. Las especies más comunes son sotoles (*Dasylirion texanum*), guapilla (*Hechtia glomerata*), agritos (*Berberis trifoliolata*), lechuguilla (*Agave lechuguilla*), espadín (*Agave striata*), amole de Castilla (*Agave bracteosa*), candelilla (*Euphorbia antisyphilitica*), tasajillo (*Opuntia leptocaulis*), pitaya de mayo (*Echinocereus enneacanthus*), nopal cegador (*Opuntia rnicrodasys*), biznaga de dulce (*Echinocactus platyacanthus*), biznaga colorada (*Ferocactus pilosus*) y nopales (*Opuntia* spp.).

Matorral Desértico Micrófilo.—Este tipo de vegetación se caracteriza por la dominancia de especies tipo arbustivo, con hojas o foliolos pequeños y a menudo aromáticos, Se encuentran abundantes cactáceas de tallos esféricos o planos; asimismo plantas tipo palma china o palma ixtlera (Yucca spp) se localizan abundantemente en terrenos planos o en abanicos aluviales de lomas o cerros en el Altiplano, en los municipios de Mier y Noriega, Dr. Arroyo, Galeana, Mina, Bustamante, García, Anáhuac y Santa Catarina. Las especies características son gobernadora (*Larrea tridentata*), hojasén (*Flourensia cernua*), mariola (*Partheniurn incanum*), albarda (*Fouquieria splendens*), afinador (*Mortonia greggii*), guayule (*Partheniurn argentatum*), comida de víbora (*Ephedra aspera*), vara resinosa (*Viguiera stenoloba*), chaparro prieto (*Acacia rigidula*), chaparro amargoso (*Castela texana*), guajillo (*Acacia berlandieri*), granjeno (*Celtis pallida*), mezquite (*Prosopis glandulosa*), mimbre (*Chilopsis linearis*), biznaga burra (*Echinocactus platyacanthus*), palma china (*Yucca filifera*), palma samandoca (*Yucca carnerosana*), nopal cegador (*Opuntia rnicrodasys*), coyonoztle (*Opuntia imbricata*), nopal rastrero (*Opuntia rastrera*), tasajillo (*Opuntia leptocaulis*) y zacatón alcalino (*Sporobolus tiroides*).

Pastizal natural.—Esta comunidad se caracteriza la ausencia de formas arboreas y arbustivas, sobresalen herbáceas graminoides con hojas delgadas y alargadas, aunque pueden combinarse en algunas otras con especies de las familias Asteraceae, Fabaceae, Brassicaceae y Chenopodiaceae. Los pastizales clímax naturales ocupan áreas reducidas en espacios abiertos dentro de los matorrales desérticos así como en situaciones edáficas específicas en lugares con mal drenaje, inundables o con excesivas sales o existencia de yeso. Este tipo de vegetación se ve reducido en la actualidad a los municipios de Galeana y Aramberri, en localidades muy específicas como "Llano de la Soledad," "La Trinidad," "EL Salero" y "La Hediondilla."

Vegetación de Ríos y Arroyos.—Estas comunidades se encuentran estrechamente ligadas a la formación orográfica de la Sierra Madre Oriental como una gran cuenca de captación con sus afluentes de ríos y arroyos, agrupa tanto a la vegetación arbórea como a la arbustiva que se encuentra en las riberas de las corrientes de agua en los municipios de Linares, Montemorelos, Allende, General Terán, Cadereyta Jiménez, Santiago, Monterrey, Guadalupe, Sabinas, Cerralvo, Lampazos y Bustamante. Estos bosques se componen por álamo de río (*Platanus occidentalis*), álamo temblón (*Populus tremuloides*), sauce (*Salix nigra*), carrizo (*Arundo donax*), culantrillo de pozo (*Adiantum capillus-veneris*), lobelia acuática (*Lobelia cardinalis*), olmo (*Ulmus crassifolia*) *y* sabino (*Taxodium mucronatum*), encontrándose abundantes especies herbáceas acuáticas o semiacuáticas, enredaderas y especies epifitas como es el paixtle (*Tillandsia usneoides*).

Estos bosques crecen principalmente en las orillas de los ríos, así como en riberas planas y amplias con drenaje superficial. Dichos sitios, humedecidos por escurrimientos perennes o esporádicos, durante largo

tiempo, permiten que las especies adquieran dimensiones en altura y diámetro mucho mayor que las que se ubican en zonas secas.

Vegetación edáfica.—Se presentan en el estado y el norte de México diversos afloramientos minerales entre los que destacan aquellos de sulfato de calcio (yeso), la importancia de estas áreas, así como un listado de especies de flora asociadas a este tipo de hábitat es presentado por Johnston (1941); este tipo de sitios se denominan comúnmente "suelos yesoso" o "hábitat gipsófilo" y se presentan por lo común en valles intermontanos del Altiplano Mexicano y en en los taludes inferiores de la Sierra Madre Oriental, en ellos se puede presentar casi cualquier tipo de asociación vegetal, sin embargo destacan entre estas, la vegetación desértica ya sea de tipo rosetófila o micrófila, las áreas de pastizal natural, es común observar también, que conforme aumenta la elevación se comienzan a presentar elementos de bosque como *Pinus* y *Quercus*, asociados a otros elementos arbustivos o semiarboreos como *Arbutus*, *Buddleja*, *Mortonia* y *Krameria*, entro otros. Para el presente estudio, cuando sea necesario a cada tipo de vegetación se agregará la denominación "gipsófilo" para denotar la presencia de yeso en el hábitat donde crece una determinada especie.

MÉTODO

Se realizaron consultas bibliográficas, así como de bases de datos de la Red Mundial de Información sobre Biodiversidad (REMIB) disponibles en la página de Internet de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO - http://www.conabio.gob.mx/remib/doctos/remib_esp.html), se generó una lista de plantas vasculares cuya distribución está restringida a los límites políticos del estado de Nuevo León y estados colindantes. Se obtuvieron datos de distribución por municipio, así como del hábitat en donde ocurren, para este último se aplica la abreviatura "ND" en caso de que la información no se especifique en las fuetes de información consultadas; su nomenclatura y sinonimia fue revisada en las bases de datos de Tropicos (Jardín Botánico de Missouri – http:/www.tropicos.org) y The Internacional Plant Names Index (Real Jardín Botánico de Kew, Herbario de la Universidad de Harvard y el Herbario Nacional de Australia – http:/www.ipni.org). El arreglo seguido para los géneros y familias, es el propuesto Mickel y Smith (2004) para el grupo de las pteridofitas, Martínez (1963) para las gimnospermas y por último para las plantas con flor se sigue el arreglo del Grupo de Filogenia de las Angiospermas (Stevens 2010).

RESULTADOS

Se presentan en el estado de Nuevo León un total de 159 especies restringidas a los límites estatales, las cuales se distribuyen en 106 géneros y 45 familias de plantas vasculares, además de cinco categorías infraespecífcas (Anexo 1). Las familias con mayor número de especies endémicas al estado son Asteraceae, Cactaceae y Lamiaceae (Tabla 1); los registros de las bases de datos consultadas indican que la distribución de las especies endémicas se da en 23 municipios del estado, donde la mayor concentración de taxa se localizan en la Sierra Madre Oriental hacia el sur y centro del estado (Fig. 2), de manera específica en el municipio de Galeana que presenta más del 50% de las especies endémicas para el estado; Los ecosistemas con mayor diversidad de especies endémicas son los bosques en sus diversas asociaciones (encino, encino – pino, pino – encino, pino y coníferas) y zonas con sustratos gipsófilos. Se registran cinco géneros cuya distribución geográfica se restringe a los límites estatales: *Aztekium*, *Digitostigma*, *Geohintonia* (Cactaceae), *Strotheria* (Asteraceae) y *Jaimehintonia* (Themidaceae), donde al menos para la familia cactaceae no se presenta una situación similar en otro estado de la República Mexicana. Solamente 13 especies cuya distribución se restringe a Nuevo León están incluidas dentro de la NOM-059-SEMARNAT-2001 (SEMARNAT 2002), una de ellas en la familia Pinaceae y el resto en Cactaceae (Anexo 1).

Al incluir taxa cuya distribución geográfica abarca además los estados vecinos de Nuevo León (Tamaulipas, Coahuila, San Luís Potosí y Zacatecas en México y Texas en los Estados Unidos de América), la cifra de especies endémicas a un nivel regional aumenta a 191, en 146 géneros y 53 familias de plantas vasculares (Anexo 2). También se registra un incremento de 6 especies protegidas por la NOM-059-SEMARNAT-2001, al ampliar el rango geográfico a los estados vecinos.

TABLA 1. Familias con mayor número de taxa endémicos a nivel regional (REG) y restringidos al estado de Nuevo León (N.L.).

Familia	**Géneros REG**	**Especies REG**	**Categorías infraespecíficas**	**Géneros NL**	**Especies N.L.**	**Categorías infraespecíficas N.L.**
Asteraceae	42	74	0	23	36	0
Cactaceae	11	21	0	10	18	4
Lamiaceae	7	16	3	6	12	1
Fabaceae	6	10	0	5	6	0
Boraginaceae	5	10	0	4	7	0
Poaceae	6	7	0	5	5	0

DISCUSION Y CONCLUSIONES

Tomando en cuenta las estimaciones hechas por Villarreal y Estrada (2008) y por Velazco (2009) para la totalidad de las especies de flora presentes en Nuevo León, las especies endemicas aquí reportadas, representan alrededor del 5 % de la flora de Nuevo Leon, la cual se alberga de manera particular en la Sierra Madre Oriental, de manera específica en los municipios de Galeana, Aramberri, General Zaragoza y Rayones, donde tan solo el municipio de Galeana presenta más de 50 % de los endemismos estatales. Esta riqueza puede atribuirse en gran medida a la variedad de hábitats y los factores climáticos presentes en la zona, los cuales van desde zonas desérticas con poca precipitación hasta el límite de la vegetación arbórea en montañas con más de 3000 metros de altitud, pasando por bosques templados y subtropicales; además de que estos tipos de vegetación han pasado por una rica historia de cambios climáticos (McDonald 1998) dando tiempo a la formación de elementos únicos o sirviendo como refugio de especies.

Por otra parte, y a pesar de los diversos trabajos florísticos que se han realizado en el estado de Nuevo León, los cuales abarcan poco más de un siglo (Velazco 2009), se ha dado poca importancia al conocimiento de las especies endémicas o con una distribución restringida a nivel regional, salvo algunos casos señalados en la normatividad federal (NOM-059-SEMARNAT-2001). Así mismo, los botánicos han dedicado pocos esfuerzos a entender las relaciones ecológicas de estas especies, su biología básica o dar un seguimiento posterior a su situación taxonómica, teniendo por ejemplo el caso de *Viguiera nesomii* Turner, la cual fue descrita a partir de un solo ejemplar (Turner 1989), de manera subsiguiente no se ha publicado nada referente a esta especie, la cual actualmente está reconocida por el "Catálogo taxonómico de especies de México" (Sarukhán et al. 2009); lo anterior nos plantea un claro ejemplo del nivel de desconocimiento de las especies endémicas y por lo general más vulnerables a extinción.

Tomando en cuenta que menos de 20 especies de este listado de endemismos estatales y regionales están incluidas en la normatividad federal bajo alguna categoría de protección, este tipo de listados, puede servir también como base para la generación de normas estatales que tengan efectos directos en la toma de decisiones por parte de las autoridades locales. Así mismo, es importante resaltar la importancia de las áreas naturales protegidas (ANPs), por ejemplo el Cerro del Potosí, declarado desde el año 2000 como un ANP de carácter estatal con una extensión de 989 has. (Anónimo 2000), lo cual se constituye como una herramienta básica para la protección de especies como *Festuca hintoniana* (Poaceae), *Potentilla leonina* (Rosaceae), y *Astranthium beamanii* (Asteraceae), entre otras que ocurren en la pradera alpina y subalpina, así como los bosques de coníferas. En este mismo rubro, el Parque Nacional Cumbres de Monterrey (de carácter federal), abarca una mayor superficie (177,395 has.) de la porción norte de la Sierra Madre Oriental, donde se destacan las siguientes especies endémicas: *Notholaena leonina* (Pteridaceae), *Agave albopilosa* (Agavaceae), *Mirandea huastecensis* (Acanthaceae) y *Lobelia sublibera* (Campanulaceae).

Las listas de especies endémicas y su categorización de acuerdo a su grado de vulnerabilidad siguiendo estándares nacionales o internacionales, debería ser una prioridad entre los botánicos de México; pero la falta de recursos humanos y materiales es uno de los principales factores que limitan esta investigación. El

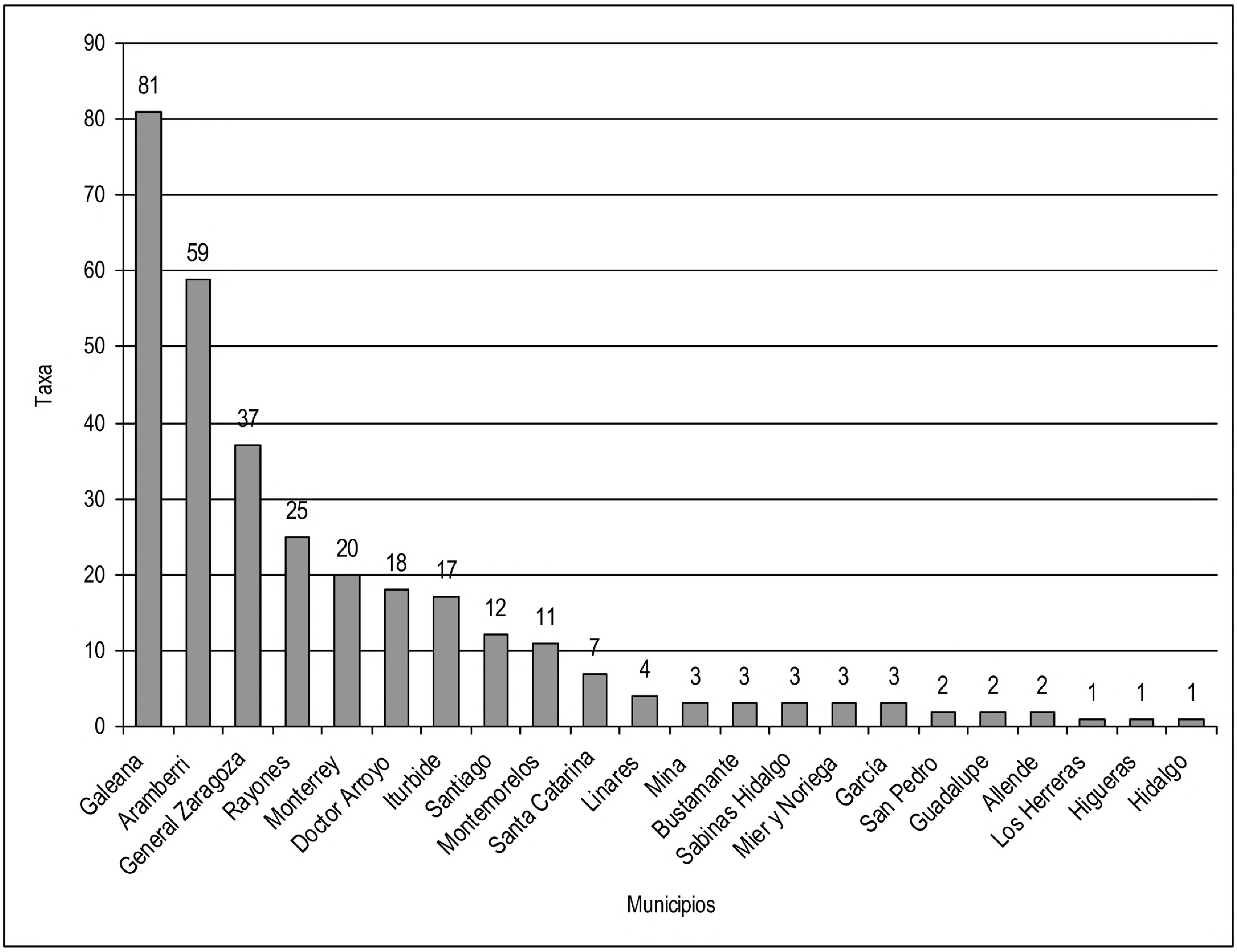

Fig. 2. Relación de taxa restringidos al estado de Nuevo León por municipio.

presente inventario, no pretende ser un trabajo extensivo ni definitivo, solo, representa una línea de partida en donde por lo menos cada cinco años se debería de revisar las especies que pueden o no ser consideradas bajo la categoría de endémicas estatales o regionales, por lo que el trabajo básico para el conocimiento florístico de cada municipio deberá de iniciar o ser retomado para constatar la permanencia o desaparición de especies según los registros históricos de los herbarios.

ANEXO 1

Lista de especies con distribucion restringida al estado de Nuevo León (N.L.), México; es señalado el hábitat y los municipios que ocupa cada especie.

PTERIDOFITAS

Aspleniaceae

Asplenium ultimum A.R.Sm., Mem. New York Bot. Gard. 88:128–129. 2004.
Distribución: Galeana, N.L.
Hábitat: rocas calizas.

Pteridaceae

Cheilanthes apiacea Mickel, Mem. New York Bot. Gard. 88:182–183. 2004.
Distribución: General Zaragoza, N.L.
Hábitat: bosques de encino y encino - pino

Cheilanthes chipinquensis Knobloch & Lellinger, Amer. Fern J. 59(1):8. 1968.
Distribución: San Pedro Garza García, N.L.
Hábitat: bosques de encino y encino - pino

Cheilanthes hintoniorum Mendenhall & G.L. Nesom, Sida 14:551. 1991.
Distribución: Aramberri, Galeana y Rayones, N.L.
Hábitat: matorral gipsófilo.

Notholaena brachycaulis Mickel, Mem. New York Bot. Gard. 88:414–415. 2004.
Distribución: Sabinas Hidalgo, N.L.
Hábitat: matorral submontano.

Notholaena leonina Maxon, Contr. U.S. Natl. Herb. 16:58. 1912.
Sinónimo: *Chrysochosma leonina* (Maxon) Pic. Serm., Webbia 43(2):308. 1989.
Distribución: Allende, Monterrey y Santa Catarina, N.L.
Hábitat: matorral submontano y bosques de encino.

Selaginellaceae
Selaginella gypsophila A.R. Sm. & T. Reeves, Sida 10(3):211. 1984.
Distribución: Galeana y Rayones, N.L.
Hábitat: matorral gipsófilo.

GIMNOSPERMAS

Pinaceae
Picea martinezii T.F. Patterson, Sida 13(2):131–135. 1988.
Distribución: Aramberri, General Zaragoza y Montemorelos, N.L.
Hábitat: bosque de coníferas.
NOM-059-SEMARNAT-2001:En Peligro (P)

LILIOPSIDA

Agavaceae
Agave albopilosa I.Cabral, Villarreal & A.E. Estrada, Act. Bot. Mex. 80:52. 2007.
Distribución: Santa Catarina, N.L.
Hábitat: matorral desértico.

Agave ovatifolia G.D.Starr & Villarreal, Sida 20(2):495–499. 2002.
Distribución: Bustamante, N.L.
Hábitat: bosque de encinos y matorral submontano.

Alliaceae
Allium hintoniorum B.L. Turner, Phytologia 75(4):333–334. 1993.
Distribución: Aramberri, Galeana, General Zaragoza e Iturbide, N.L.
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Hábitat: bosques de encino, pino y coníferas.

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Hábitat: matorral, Cerro Peña Nevada.

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Hábitat: Matorral submontano.

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Hábitat: llano gipsófilo.

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Hábitat: Bosque de encino.

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Hábitat: Matorral desértico.

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Sinónimo: *Escobaria roseana* subsp. *galeanensis* Haugg, Kakteen Sukk. 46:76. 1995.
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Hábitat: vegetación gipsófila.
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Hábitat: matorral desértico.
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Hábitat: matorral gipsófilo.
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Hábitat: vegetación semidesértica.
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Hábitat: matorral gipsófilo.
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Hábitat: matorral desértico.
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Hábitat: matorral desértico.
NOM-059-SEMARNAT-2001:En Peligro (P)

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Distribución: Galeana, N.L.
Hábitat: pastizales en bosques de pino piñonero.
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Distribución: Aramberri y Galeana, N.L.
Hábitat: matorral y bosque de pino.

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Hábitat: matorral desértico.

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Hábitat: matorral desértico.

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Hábitat: matorral gipsófilo.

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Sinónimo: *Turbinicarpus schmiedickeanus* var. *dickisoniae* Glass & R.A. Foster, Cact. Succ. J. 54(2):74. 1982.
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Hábitat: matorral desértico.

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Distribución: Aramberri, N.L.
Hábitat: matorral desértico.
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Turbinicarpus hoferi Lüthy & A.B. Lau, Kakteen Sukk. 42(2):37. 1991.
Distribución: Aramberri, N.L.
Hábitat: matorral gipsófilo.
NOM-059-SEMARNAT-2001:Amenazada (A)

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Distribución: Hidalgo, N.L.
Hábitat: matorral semidesértico.

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Hábitat: matorral desértico.
NOM-059-SEMARNAT-2001:Amenazada (A)

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Sinónimo: *Gymnocactus subterraneus* var. *zaragozae* Glass & R.A. Foster, Cact. Succ. J. 50(6):283. 1978.
Distribución: General Zaragoza, N.L.
Hábitat: matorral desértico gipsófila.

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Sinónimos: *Heterotoma pringlei* B.L. Rob. Proc. Amer. Acad. Arts 44(21):615. 1909; *Lobelia gypsophila* T.J. Ayers, Sida 13:144. 1988.
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Hábitat: matorral gipsófilo.

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Distribución: Aramberri y Galeana, N.L.
Hábitat: vegetación gipsófolia.

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Hábitat: matorral gipsófilo.

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Distribución: Mina, N.L.
Hábitat: vegetación desértica.

Paronychia hintoniorum B.L. Turner, Phytologia 79(1):38. 1995
Distribución: Galeana, N.L.
Hábitat: matorral desértico.

Crassulaceae
Sedum booleanum B.L. Turner, Phytologia 79(1):31. 1995.
Distribución: Rayones, N.L.
Hábitat: matorral gipsófilo.

Sedum hintoniorum B.L. Turner, Phytologia 78(6):405. 1995.
Distribución: Aramberri y General Zaragoza, N.L.
Hábitat: bosque de encino, encino – pino y coníferas.

Euphorbiaceae
Euphorbia correlli M.C. Johnst., Wrightia 5(5):130. 1975.
Sinónimo: *Tithymalus correllii* (M.C. Johnst.) Soják, Čas. Nár. Mus., Odd. Přír. 148:199. 1979
Distribución: Galeana, N.L.
Hábitat: matorral gipsófilo.

Euphorbia neilmulleri M.C. Johnst., Wrightia 5(5):125. 1975.
Sinónimo: *Tithymalus neilmulleri* (M.C. Johnst.) Soják, Čas. Nár. Mus., Odd. Přír. 148:199. 1979
Distribución: Armaberri, Galeana, General Zaragoza, Linares y Rayones, N.L.
Hábitat: bosque de pinos gipsófilo.

Fabaceae
Astragalus mario-sousae A.E. Estrada, Villareal & Yen-Mendez, Brittonia 57(4):315. 2005.
Distribución: Santa Catarina, N.L.
Hábitat: ND.

Astragalus regiomontanus Barneby, Mem. New York Bot. Gard. 13:168–169. 1964.
Distribución: Linares, Montemorelos y Monterrey, N.L.
Hábitat: matorral semidesértico.

*Lupinus hintoniorum*B.L. Turner, Phytologia 76(4):295. 1994.
Distribución: Aramberri, Doctor Arroyo y General Zaragoza, N.L.
Hábitat: bosque de encino, pino y coníferas.

Myrospermum sousanum A. Delgado & M.C. Johnst., Syst. Bot. 9:356. 1984.
Distribución: Bustamante, N.L.
Hábitat: matorral submontano y boque de encino.

Phaseolus novoleonensis Debouck, Novon 16(1):105–111. 2006.
Distribución: Iturbide y Linares, N.L.
Hábitat: matorral y bosque encino – nogal.

Sophora juanhintoniana B.L. Turner, Phytologia 76:385. 1994.
Distribución: Aramberri, N.L.
Hábitat: matorral gipsófilo.

Frankeniaceae
Frankenia gypsophila I.M. Johnst., J. Arnold Arbor. 20:237. 1939.
Distribución: Galeana, N.L.
Hábitat: pastizal gipsófilo.

Gentianaceae
Geniostemon gypsophilum B.L. Turner, Phytologia 76(1):11–13. 1994.
Distribución: Aramberri, Doctor Arroyo, Galeana y Mier y Noriega, N.L.
Hábitat: matorral gipsófilo.

Gentiana hintoniorum B.L. Turner, Phytologia 80(2):118. 1996.
Distribución: Aramberri, N.L.
Hábitat: bosque de pino – encino.

Lamiaceae
Hedeoma ciliolata (Epling) R.S. Irving, Brittonia 22:345. 1970.
Distribución: Doctor Arroyo, Galeana e Iturbide, N.L.
Hábitat: matorral gipsófilo, bosque de pinos.

Hedeoma palmeri var. *galeana* B.L. Turner, Phytologia 71(1):33–34. 1991.
Distribución: Galeana e Iturbide, N.L.
Hábitat: bosque de encinos

Hedeoma pusilla (R.S. Irving) R.S. Irving, Brittonia 22:345. 1970.
Distribución: Galeana, N.L.
Hábitat: ND.

Hedeoma quercetorum Epling, Repert. Spec. Nov. Regni Veg. Beih. 115:41. 1939.
Distribución: Aramberri y Galeana, N.L.
Hábitat: matorral.

Monarda pringlei Fernald, Proc. Amer. Acad. Arts 36(27):501. 1901.
Distribución: Monterrey y Santiago, N.L.
Hábitat: matorral y bosque de encino y pino.

Poliomintha bustamanta B.L. Turner, Phytologia 74:164. 1993.
Distribución: Bustamante, N.L.
Hábitat: matorral semidesértico.

Salvia jaimehintoniana Ramamoorthy ex B.L. Turner, Phytologia 79(2):97. 1995.
Distribución: Doctor Arroyo, General Zaragoza, Iturbide y Santiago, N.L.
Hábitat: bosque de encino y bosque de pino.

Salvia jorgehintoniana Ramamoorthy ex B.L. Turner, Phytologia 79(2):80. 1995.
Distribución: Doctor Arroyo, General Zaragoza, Iturbide y Santiago, N.L.
Hábitat: bosque de encino – pino.

Satureja hintoniorum B.L. Turner, Phytologia 75(5):411. 1993.
Distribución: Aramberri, Doctor Arroyo y General Zaragoza, N.L.
Hábitat: matorral desértico y bosque de encino.

Scutellaria aramberrana B.L. Turner, Phytologia 76(5):352. 1994.
Distribución: Aramberri, N.L.
Hábitat: bosque de encino y encino – pino.

Scutellaria hintoniorum Henrickson, Aliso 12(3):517–519. 1989.
Distribución: Galeana, N.L.
Hábitat: matorral gipsófilo, pinos.

Scutellaria lutilabia T.M. Lane & G.L. Nesom, Madroño 35(2):112–114. 1988.
Distribución: Aramberri, Galeana y General Zaragoza, N.L.
Hábitat: matorral gipsófilo.

Scutellaria monterreyana B.L. Turner, Phytologia 76:368. 1994.
Distribución: Montemorelos, Monterrey, Santa Catarina y Santiago, N.L.
Hábitat: bosque de encino, encino – pino y coníferas.

Lentibulariaceae
Pinguicula immaculata Zamudio & Lux, Acta Bot. Mex. 20:40–44, f. 1–2. 1992.
Distribución: Aramberi, Galeana, General Zaragoza y Rayones, N.L.
Hábitat: matorral gipsófilo.

Linaceae
Linum gypsogenium G.L. Nesom, Madroño 30:252. 1983.
Distribución: Doctor Arroyo, N.L.
Hábitat: matorral gipsófilo.

Linum modestum C.M. Rogers, Rhodora 66:406. 1964. Distribución: Aramberri, Galeana y Rayones, N.L.
Hábitat: matorral gipsófilo.

Loasaceae
Mentzelia hintoniorum B.L. Turner & A.L.Hempel, Phytologia 79(4):298. 1995.
Distribución: Galeana, N.L.
Hábitat: matorral gipsófilo.

Nyctaginaceae
Mirabilis nesomii B.L. Turner, Phytologia 70(1):44. 1991.

Distribución: Aramberri, Doctor Arroyo, Galeana y Santiago, N.L.
Hábitat: matorral gipsófilo.

Oleaceae
Menodora gypsophila B.L. Turner, Phytologia 79(1):8. 1995
Distribución: Galeana y Rayones, N.L.
Hábitat: matorral gipsófilo y bosque de pino piñonero.

Onagraceae
Oenothera stubbei W. Dietr. & P.H. Raven, Syst. Bot. 10(1):41. 1985
Distribución: Galeana y Santiago, N.L.
Hábitat: bosque de pino gipsófilo.

Papaveraceae
Argemone subalpina J.A. McDonald, Brittonia 43(2):120–122. 1991.
Distribución: General Zaragoza, N.L.
Hábitat: pradera subalpina.

Hunnemannia hintoniorum G.L. Nesom, Phytologia 73(4):335. 1992.
Distribución: Galeana, N.L.
Hábitat: matorral gipsófilo.

Orobanchaceae
Agalinis gypsophila B.L. Turner, Phytologia 59(5):319. 1986.
Distribución: Galeana e Iturbide, N.L.
Hábitat: matorral gipsófilo.

Castilleja galehintoniae G.L. Nesom, Phytologia 72(3):246. 1992.
Distribución: Aramberri y Galeana, N.L.
Hábitat: matorral gipsófilo, bosque de pino.

Seymeria deflexa Eastw., Proc. Amer. Acad. Arts 44:607. 1909.
Distribución: García, Monterrey, Santa Catarina y Santiago, N.L.
Hábitat: bosque de encino – pino.

Plantaginaceae
Penstemon galloensis G.L. Nesom, Phytologia 71(5):335. 1991.
Distribución: Aramberri, Galeana, General Zaragoza y Montemorelos, N.L.
Hábitat: bosque de encino, encino – pino y pino.

Polygonaceae
Eriogonum fimbriatum W.J. Hess & Reveal, Great Basin Naturalist 36(3):308–310. 1976.
Distribución: Galeana, N.L.
Hábitat: matorral desértico.

Eriogonum turneri Reveal, Sida 5(4):265–267. 1974.
Distribución: Galeana, N.L.
Hábitat: pastizal gipsófilo.

Rosaceae
Cercocarpus mexicanus Henrickson, Syst. Bot. 12(2):293. 1987.
Distribución: Doctor Arroyo y Galeana, N.L.
Hábitat: matorral submontano.

Rubiaceae
Galium juniperinum Standl., Publ. Field Columbian Mus., Bot. Ser. 22(2):114. 1940.
Distribución: Galeana y Rayones, N.L.
Hábitat: matorral gipsófilo.

Galium pringlei Greenm., Proc. Amer. Acad. Arts 33(25):458–459. 1898.
Distribución: Montemorelos, Monterrey y Santiago, N.L.
Hábitat: bosque de encino y bosque de pino.

Scrophulariaceae
Leucophyllum alejandrae G.L. Nesom, Phytologia 74(4):293–294. 1993.
Distribución: Aramberri y Galeana, N.L.
Hábitat: matorral gipsófilo.

Leucophyllum hintoniorum G.L. Nesom, Phytologia 71(5):337–338. 1991
Distribución: Aramberri y General Zaragoza, N.L.
Hábitat: matorral gipsófilo.

Solanaceae
Lycianthes hintonii E.A. Dean, Bot. J. Linn. Soc. 145(4):407–408. 2004
Distribución: Aramberri, N.L.
Hábitat: matorral desértico.

Physalis hunzikeriana M. Martínez, Kurtziana 27(2):383–385, f. 1. 1999
Distribución: Aramberri y General Zaragoza, N.L.
Hábitat: bosque de encino y encino – pino.

Physalis muelleri Waterf., Rhodora 69(777):115. 1967.
Distribución: Monterrey y Santa Catarina, N.L.
Hábitat: matorral desértico.

Verbenaceae
Glandularia alejandrana B.L. Turner, Lundellia 2:57. 1999.
Distribución: Galeana, N.L.
Hábitat: llanos gipsófilos.

ANEXO 2

Lista de taxa con distribucion restringida al estado de Nuevo León y estados vecinos.

PTERIDOFITAS

Pteridaceae
Notholaena bryopoda Maxon, Proc. Biol. Soc. Wash. 18(38):205–206. 1905.
Sinónimo: *Cheilanthes bryopoda* (Maxon) Domin, Biblioth. Bot. 85(1):133. 1913.
Distribución: Aramberri, Doctor Arroyo, Galeana y General Zaragoza, N.L.; General Cepeda, Coah.
Hábitat: matorral gipsófilo y rocas calizas.

GIMNOSPERMAS

Pinaceae

Pinus culminicola Andresen & Beaman, J. Arnold Arbor. 42:438. 1961.
Distribución: Galeana, General Zaragoza y Rayones, N.L.; Arteaga, Coah.
Hábitat: bosque de coníferas y pradera alpina.
NOM-059-SEMARNAT-2001:Protección Especial (Pr)

LILIOPSIDA

Agavaceae

Agave bracteosa S. Watson ex Engelm., Gardener's chronicle, new series 18:776. 1882.
Distribución: Montemorelos y Santa Catarina, N.L.; Castaños, Coah.
Hábitat: rocas calizas, matorral desértico rosetofilo
NOM-059-SEMARNAT-2001:Amenazada (A)

Agave montana Villarreal, Sida 17(1):191. 1996.
Distribución: Rayones, N.L.; Arteaga, Coah.
Hábitat: bosque de coníferas y vegetación subalpina.

Yucca linearifolia Clary, Brittonia 47(4):394. 1995.
Distribución: Galeana y Rayones, N.L.; Ramos Arizpe, Coah.
Hábitat: matorral submontano y desértico.

Hypoxidaceae

Hypoxis pulchella G.L. Nesom, Phytologia 75(5):377. 1993.
Distribución: Montemorelos y Santiago, N.L.; Hidalgo, Tamps.
Hábitat: bosque encino- pino.

Orchidaceae

Malaxis hintonii Todzia, Orquídea (Mexico City), n.s., 13(1–2):121, f. 1. 1993.
Sinónimo: *Tamayorkis hintonii* (Todzia) R. González & Szlach., Ann. Bot. Fenn. 35(1):22. 1998.
Distribución: Galeana, Santiago, Santa Catarina, N.L.; Arteaga, Coah.; Tamps.; Tamps.
Hábitat: bosque de pino – encino y bosque coníferas.

Poaceae

Bromus densus Swalllen, Contr. U.S. Natl. Herb. 29(9):396.1950.
Sinónimo: *Bromopsis densa* (Swallen) Holub, Folia Geobot. Phytotax. 8(2):167. 1973.
Distribución: General Zaragoza, N. L.; Arteaga y Saltillo, Coah. y Tamaulipas.
Hábitat: bosque de pino y bosque de coníferas.

Festuca valdesii M. Gonzalez-Ledezma & S. D. Koch. Novon 8:149.1998.
Distribución: General Zaragoza y Rayones, N.L.; Arteaga, Coah. y Tamaulipas.
Hábitat: bosque de coníferas.

Ruscaceae

Dasylirion miquihuanense Bogler, Brittonia 50(1):76. 1998.
Distribución: Doctor Arroyo, N.L.; Miquihuana, Tamps.
Hábitat: matorral desértico rosetófilo.

Dasylirion quadrangulatum S. Watson, Proc. Amer. Acad. Arts 14:250. 1879.
Distribución: Aramberri, Doctor Arroyo y Mier y Noriega, N.L.; Miquihuana y Tula, Tamps.
Hábitat: matorral desértico rosetófilo.
NOM-059-SEMARNAT-2001:Amenazada (A)

Nolina nelsonii Rose, Contr. U.S. Natl. Herb. 10:92. 1906.
Distribución: Aramberri y General Zaragoza, N.L.; Miquihuana y Tula, Tamps.
Hábitat: chaparral, bosque de encinos.

MAGNOLIOPSIDA

Amaranthaceae

Suaeda palmeri (Standl.) Standl., Publ. Field Columbian Mus., Bot. Ser. 8(1):10. 1930.
Sinónimo: *Dondia palmeri* Standl., North American Flora 21(1):91. 1916.
Distribución: Aramberri y Mina, N.L.; Parras, Coah. y Concepción del Oro, Zac.
Hábitat: matorral desértico.

Anacardiaceae

Rhus muelleri Standl. & F.A. Barkley, Ann. Missouri Bot. Gard. 24(4):359. 1937.
Distribución: Aramberri, Galeana, General Zaragoza, Linares y Montemorelos, N.L.; Arteaga, Coah.
Hábitat: matorral submontano y bosque de encino.

Apiaceae

Arracacia schneideri Mathias & Constante, Bull. Torrey Bot. Club 69(2):151. 1942.
Distribución: Aramberri, Galeana y General Zaragoza, N.L.; Arteaga, Coah; Hidalgo, Tamps.
Hábitat: bosque de encino, pino y coníferas.

Tauschia hintoniorum Constance & Affolter, Syst. Bot. 12(2):286. 1987.
Distribución: Rayones, N.L.; Arteaga, Coah.
Hábitat: bosque de pinos.

Tauschia infernicola Constance & Affolter, Syst. Bot. 12(2):289. 1987.
Distribución: Aramberri, Galeana y General Zaragoza, N.L.; Arteaga, Coah.
Hábitat: bosque de encino – pino.

Aristolochiaceae

Aristolochia lassa I.M. Johnst., J. Arnold Arbor. 21:255. 1940.
Distribución: Allende y Galeana, N.L.; Saltillo, Coah.
Hábitat: ND

Asteraceae

Ageratina campyloclada (B.L. Rob.) R.M. King & H. Rob., Phytologia 19:220. 1970.
Sinónimos: *Eupatorium campylocladum* B.L. Rob. Proceedings of the Boston Society of Natural History 31:247. 1904. Distribución: Galeana, N.L.; Arteaga, Coah.
Hábitat: bosque de pino.

Ageratina gypsophila B.L. Turner, Phytologia 57:130. 1985.
Distribución: Galeana, N.L.; Coah.
Hábitat: Bosque gipsófilos de encino, pino y coníferas.

Ageratina ilicifolia B.L. Turner, Phytologia 71(4):311. 1991.
Distribución: Rayones, N.L.; Coah.
Hábitat: matorral submontano.

Astranthium beamanii DeJong, Publ. Mus. Michigan State Univ., Biol. Ser. 2(9):514–517. 1965.
Distribución: Galeana, N.L.; Arteaga, Coah.; Tamps.
Hábitat: bosques de pino, encino, coníferas, pradera alpina y subalpina.

Bahia autumnalis Ellison, Rhodora 66:199. 1964.
Distribución: Aramberri, Doctor González, Galeana, Iturbide, Linares, Rayones, Sabinas Hidalgo, Santa Catarina y Santiago, N.L.; Arteaga y Saltillo, Coah.
Hábitat: matorral, chaparra, bosque de encino – pino, vegetación ruderal.

Bidens longistyla C.R. Hart, Syst. Bot. 30:289–292. 1978.
Distribución: Aramberri y Galeana, N.L.; Arteaga, Castaños, Ocampo, Ramos Arizpe, Saltillo, Coah.
Hábitat: bosque de encino, pino y coníferas.

Brickellia hintoniorum B.L. Turner, Phytologia 58(7):493–494. 1985.
Sinónimo: *Phanerostylis hintoniorum* (B.L. Turner) R.M. King & H. Rob., Phytologia 60:80. 1986.
Distribución: Galeana, General Zaragoza, N.L.; Arteaga, Coah.
Hábitat: bosque de pino y encino – pino.

Brickellia nesomii B.L. Turner, Brittonia 30:342. 1978.
Sinónimo: *Phanerostylis nesomii* (B.L. Turner) R.M. King & H. Rob., Phytologia 48:221. 1981.
Distribución: Galeana, N.L.; Arteaga, Coah.; Tamps.
Hábitat: bosque de pino y junipero

Brickellia urolepis S.F. Blake, J. Wash. Acad. Sci. 32:146. 1942.
Distribución: Santa Catarina, N.L.; Acuña, Cuatro Ciénegas, Muzquiz y Ramos Arizpe, Coah.
Hábitat: bosque de encino – pino.

Chaptalia lyratifolia Burkart, Darwiniana 6(4):527–529, f. 3. 1944.
Distribución: Aramberri, Doctor Arroyo, Monterrey, Rayones, Santa Catarina y Santiago, N.L.; Arteaga y Ramos Arizpe, Coah.; Miquihuana, Tamps.
Hábitat: bosque de encino y pino.

Dahlia foeniculifolia Sherff, Amer. J. Bot. 38(1):71. 1951.
Distribución: General Zaragoza, N.L.; Tamps.
Hábitat: bosque de pino y pino – encino.

Dahlia tubulata P.D. Sorensen, Rhodora 82:353–360. 1980.
Distribución: Aramberri, Cerralvo, Doctor Arroyo, Galeana, General Zaragoza, Montemorelos y Rayones, N.L.; Arteaga, General Cepeda, Coah.; Tamps.; Zac.
Hábitat: bosque de encinos y pino.

Erigeron onofrensis G.L. Nesom, Phytologia 66:491. 1989.
Distribución: General Zaragoza, N.L.; Tamps.
Hábitat: bosque de pino.

Flourensia monticola M.O. Dillon, Southw. Naturalist 21:147. 1976.
Distribución: Montemorelos, Monterrey, San Pedro Garza García, Santiago y Santa Catarina, N.L.; Arteaga y Ramos Arizpe, Coah.
Hábitat: bosque de pino, encino y coníferas.

Gnaphalium hintoniorum G.L. Nesom, Phytologia 68(5):414. 1990.
Distribución: Doctor Arroyo, Galeana, General Zaragoza, Rayones N.L.; Arteaga, Coah.
Hábitat: bosque de pino, encino y coníferas.

Gutierrezia grandis S.F. Blake, Contr. U.S. Natl. Herb. 22(8):592–593, pl. 55. 1924.
Sinónimo: *Xanthocephalum grande* (S.F. Blake) Shinners Field & Laboratory 18(1):28. 1950.
Distribución: Galeana, N.L.; Arteaga y Ramos Arizpe, Coah.
Hábitat: matorrales y bosque de encino.

Koanophyllon reyrobinsonii B.L. Turner, Phytologia 52:495. 1983.
Sinónimo: Eupatorium reyrobinsonii (B.L. Turner) B.L. Turner, Phytologia 67:388. 1989.
Distribución: Aramberri, Iturbide, Linares, Monterrey, Montemorelos, San Pedro Garza García, Santiago N.L.; Aldama, Hidalgo, San carlos y Victoria Tamps.
Hábitat: boque de pino y encino – pino.

Machaeranthera johnstonii (S.F. Blake) B.L. Turner, Amer. J. Bot. 60:837. 1973.
Sinónimos: *Haplopappus johnstonii* S.F. Blake, Proc. Biol. Soc. Wash. 54:18. 1941; *Xanthisma johnstonii* (S.F. Blake) D.R. Morgan & R.L. Hartm., Sida 20(4):1404. 2003.
Distribución: Mina, N.L.; Cuatro Ciénegas, Escobedo y Monclova, Coah.
Hábitat: matorral desértico.

Machaeranthera crutchfieldii B.L. Turner, Phytologia 26:116. 1973.
Sinónimo: *Xylorhiza crutchfieldii* (B.L. Turner) D.R. Morgan & R.L. Hartm., Sida 20(4):1403. 2003.
Distribución: Doctor Arroyo y Galeana, N.L.
Hábitat: matorral, bosque de encino y pino.

Machaeranthera heterophylla R.L. Hartm., Phytologia 68:445. 1990.
Sinónimos: *Machaeranthera rhizomata* A. Nelson & J.F. Macbr., Botanical Gazette 62(2):148. 1916; *Haplopappus rhizomatus* M.C. Johnst., Rhodora 63:177. 1961.
Distribución: Galeana, N.L.; Coah.
Hábitat: pastizal gipsófilo.

Melampodium argophyllum (A. Gray ex B.L. Rob.) S.F. Blake, Contr. U.S. Natl. Herb. 22(8):606. 1924.
Sinónimo: *Melampodium cinereum* var. *argophyllum* A. Gray ex B.L. Rob., Proc. Amer. Acad. Arts 36:458. 1901.
Distribución: Galeana, Mina, Monterrey, Salinas Victoria y Santa Catarina, N.L.; Castaños, Cuatro Ciénegas, General Cepeda, Parras y Saltillo, Coah.
Hábitat: matorral desértico.

Packera hintoniorum (B.L. Turner) C. Jeffrey, Kew Bull. 47(1):101. 1992.

Sinónimo: *Senecio hintoniorum* B.L. Turner, Phytologia 57:378. 1985.
Distribución: Galeana, General Zaragoza y Rayones, N.L.; Coah.; Tamps.
Hábitat: bosque de encino, chaparal, pradera alpina.

Packera montereyana (S. Watson) C. Jeffrey, Kew Bull. 47(1):101. 1992.
Sinónimo: *Senecio montereyanus* S. Watson, Proc. Amer. Acad. Arts 25:155. 1890.
Distribución: Guadalupe, Monterrey y Santiago, N.L.; Ramos Arizpe, Coah.; San Carlos, Tamps.
Hábitat: matorral y bosque de encino-pino.

Plateilema palmeri (A. Gray) Cockerell, Bull. Torrey Bot. Club 31(9):462. 1904.
Sinónimo: *Actinella palmeri* A. Gray, Proc. Amer. Acad. Arts 19:31. 1883.
Distribución: Galeana, N.L.; Ocampo y Saltillo, Coah.
Hábitat: llanos gipsófilos.

Porophyllum amplexicaule Engelm. ex A. Gray, Smithsonian Contributions to Knowledge 3(5):120. 1852.
Distribución: Doctor Arroyo, Galeana, Mina, Rayones y Santa Catarina, N.L.; Arteaga, Ramos Arizpe y Saltillo, Coah.
Hábitat: matorral desértico.

Psilactis odysseus (G.L. Nesom) D.R. Morgan, Syst. Bot. 18(2):298. 1993.
Sinónimo: *Machaeranthera odysseus* G.L. Nesom, Syst. Bot. 3(2):218, f. 1–2. 1978.
Distribución: Doctor Arroyo y General Zaragoza, N.L.; Miquihuana, Tamps.
Hábitat: bosque coníferas y vegetación subalpina.

Ratibida coahuilensis B.L. Turner, Sida 13:35 (–37). 1988.
Distribución: Bustamante, N.L.; Acuña, Muzquiz y Ocampo, Coah.
Hábitat: matorral submontano.

Roldana nesomiorum (B.L. Turner) C. Jeffrey, Kew Bull. 47(1):55. 1992.
Sinónimo: *Senecio nesomiorum* B.L. Turner, Phytologia 66(6):467. 1989.
Distribución: Doctor Arroyo y General Zaragoza, N.L.; Tamps.
Hábitat: bosque de encino.

Roldana sundbergii (B.L. Turner) B.L. Turner, Phytologia 80(4):278. 1996.
Sinónimo: *Senecio sundbergii* B.L. Turner, Brittonia 37(1):117, f. 1. 1985.
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Hábitat: bosque de encino – pino y vegetación riparia.

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DIODIA SAPONARIIFOLIA (RUBIACEAE: SPERMACOCEAE), ESPECIE DISYUNTA ENTRE SUDAMÉRICA Y MÉXICO

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ABSTRACT

Diodia saponariifolia (Cham. & Schltdl.) K. Schum. (Rubiaceae), known only from South America in the past, has been recorded for Puebla and Veracruz, Mexico. Specimens of this species had been wrongly identified as *Diodia maritima* Thonn.

Key Words: *Diodia*, South America, Mexico, disjunction

RESUMEN

Diodia saponariifolia (Cham. & Schltdl.) K. Schum. (Rubiaceae), conocida previamente sólo de Sudamérica, se registra para Puebla y Veracruz, México. Especímenes de esta especie se habían identificado erróneamente como *Diodia maritima* Thonn.

Palabras clave: *Diodia*, Sudamérica, México, disyunción

INTRODUCCIÓN

Diodia L. s. str. (Rubiaceae: Spermacoceae), comprende cinco especies americanas, distribuidas principalmente en terrenos húmedos, anegados, pantanosos o arenosos, bordes de arroyos, lagunas o ríos. Son hierbas postradas, rastreras, de hojas opuestas con vainas estipulares casi siempre bien desarrolladas, sus flores axilares, 1 a 5, isomorfas, con corolas infundibuliformes, de lóbulos pilosos en la superficie interna, estilo y ramas estigmáticas filiformes y frutos indehiscentes (Bacigalupo y Cabral 1999).

Diodia saponariifolia (Cham. & Schltdl.) K. Schum., se conocía únicamente de Sudamérica, en particular de Brasil, Paraguay y recientemente de Argentina en los límites con Brasil. En el presente trabajo se registra su presencia en los estados de Puebla y Veracruz, México. Varios especímenes colectados desde 1974 en el estado de Veracruz, y depositados en los herbarios ENCB, MEXU y XAL, se habían identificado erróneamente como *Diodia maritima* Thonn. (sinónimo de *Diodia serrulata* (P. Beauv.) G. Taylor), y más recientemente ha sido considerada como *Diodella serrulata* (P. Beauv.) Borhidi, (Borhidi 2006). *Diodia maritima* Thonn. se describió de África y su distribución se ha extendido a algunas playas del Caribe, Belice, Guatemala y Nicaragua (Burger & Taylor 1993; Standley & Williams 1975; Taylor 2001). Se caracteriza por tener 4 sépalos y estigmas capitados; a diferencia de los especímenes examinados que poseen 2(3) sépalos y estilos bífidos con ramas estigmáticas filiformes.

Diodia saponariifolia (Cham. & Schltdl.) K. Schum., in Martius, Fl. Bra. 6(6):16. 1889. (**Fig. 1**). *Borreria saponariifolia* Cham. & Schltdl., Linnaea 3:325. 1828. Tipo: BRASIL: Rio de Janeiro, Restinga de Cabo Frio, *D. Sucre, G. Barroso, C.L. Ichase & R. Reitz 4928* (neotipo: RB; isoneotipo: SI, US) Neotipo seleccionado por Bacigalupo & Cabral, Darwiniana 37:157. 1999.

Hierbas rastreras, suculentas; tallos verdes a rojizos en algunas partes en fresco, oscuros cuando secos, teretes, de hasta 2 m de largo, de 4–6 mm de diámetro, glabros, con entrenudos de 2–7 cm de largo; estípulas unidas en una vaina estipular, blanco verdosa en fresco y café claro en seco, de 6–9 mm de largo, glabras, con 3 setas rojizas, glandulares en el ápice, triangulares, la central de 4–5 mm de largo, las laterales de 0.3–1.5 mm, glabras en el dorso, ciliadas en el margen, alternando con coléteres en la base. Hojas opuestas y decusadas, subsésiles, pecíolos de ca. 1 mm de largo; oblanceoladas a elípticas, ápice agudo a muy corto acuminado, margen rojizo, entero, estrigiloso, gradualmente adelgazándose a hacia la base, redondeada en la base, de

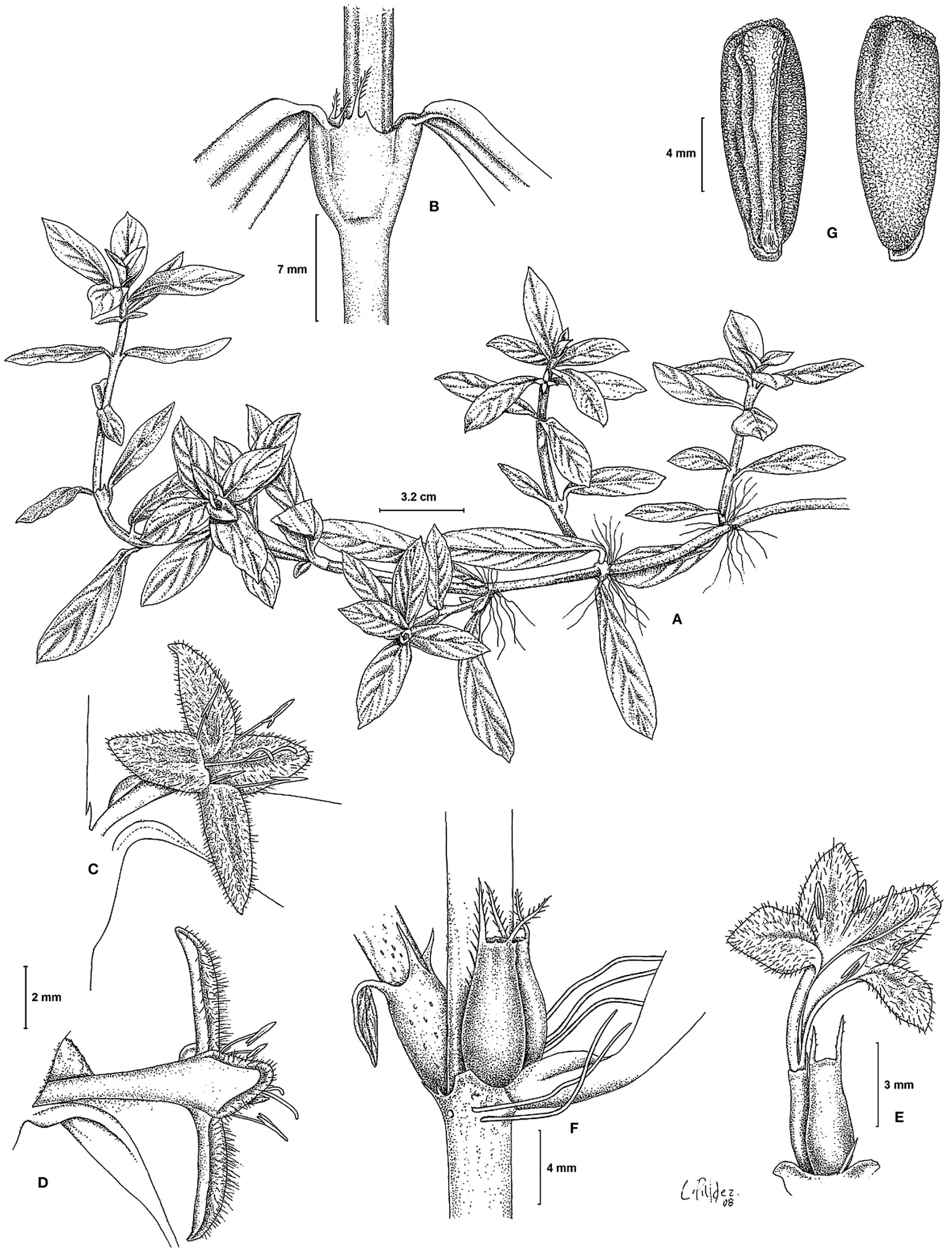

Fig. 1. ***Diodia saponariifolia*. A,** rama con flores y raíces en los nudos; **B,** vaina interpeciolar; **C, D,** flores axilares con diferente orientación; **E,** corola con un corte longitudinal y un ovario; **F,** frutos expuestos en la axila de un nudo y algunas raíces; **G,** semillas en vista ventral y dorsal.

3–7 cm de largo y 0.8–1.8 cm de ancho, crasas cuando frescas, pinnado nervadas, con 4–5 pares de nervios secundarios, ambas superficies glabras, la vena media prominente por abajo, muy esparcidamente estrigosa a lisa. Flores axilares, 2 por axila; cada par contenido entre 2 bractéolas, lanceoladas, de hasta 2 mm de largo, ligeramente unidas en la base; hipantio oblongo ovoide, comprimido, de 5–5.5 mm de largo y 1.5–2 mm de ancho, liso, glabro, tubo del cáliz ca. 0.5 mm de largo, lóbulos del cáliz 2, muy raramente 3, lanceolados, de 1.5–2.5 mm de largo y 0.8–1 mm de ancho, glabros en el dorso y ciliados en el margen, el margen del tubo del cáliz y la base de los lóbulos con coléteres o dientecillos. *Corola* infundibuliforme, blanca, tubo estrecho, de 5–6 mm de largo y ca. 1.2 mm de diámetro, glabro por fuera y por dentro, lóbulos 4, elípticos a elíptico ovados, de 4–5 mm de largo y 2–3 mm de ancho, el margen reflejo cuando fresco, glabros en el dorso, con tricomas largos, lisos (no moniliformes), dispersos en la superficie interna; estambres 4, exertos, filamentos de 1.5–2 mm de largo, anteras dorsifijas, oblongas, de 1.5–1.8 mm de largo; estilo filiforme, bifido, exerto, de 1.1–1.3 cm de largo, ramas estigmáticas filiformes, de 3–3.5 mm de largo. Frutos ovoides, comprimidos, completamente ocultos por la vaina estipular, de 7–8 mm de largo y ca. 3 mm de ancho, lisos, glabros. Semillas ca. 7 mm de largo, reticulado foveolada, cara ventral con un surco.

Ejemplares examinados: **MÉXICO. Puebla:** Municipio Hueytamalco, Campo Experimental Las Margaritas, Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), 19°56'46" N, 97°18'40" W, 14 Abr 2008, *G. Cornejo, G. Ibarra & N. González 2597* (MEXU). **Veracruz:** Municipio Catemaco, 2 km de terracería Tebana Bastonal, 25 Nov 1978, *A. Gómez Pompa 5351* (XAL); Camino Bastonal a Santa Martha, 26 Nov 1978, *A. Gómez Pompa & I. Calzada 5488* (MEXU, XAL); Tebana a Miguel Hidalgo, 14 Sep 2008, *L. Lozada & C. Gallardo 3542* (FCME, MEXU, XAL); Catemaco, 25 Jul 1974, *L.W. Boege 3196* (MEXU). Municipio Hidalgotitlán, A lo largo del río Cuechapa, después del Roble y antes de la colonia Rodolfo Sánchez Taboada, 29 Oct 1983, *M. Cházaro 3308* (XAL). Municipio Ixhuatlán de Madero, El Campo, 23 Feb 1974, *F. Ponce 171* (ENCB, XAL). Municipio Mecayapan, 2 km SE del ejido La Valentina. 18°17' N y 94°45' W, 30 Mar 1995, *M. Vázquez 4617* (XAL). Municipio San Andrés Tuxtla, Balzapote, 4 Nov 1992, *D. Liesenfeld 47* (XAL). Municipio Soteapan, Arroyo Claro, 12 May 1981, *J. Palma 619* (XAL).

Existen diferencias entre las poblaciones sudaméricanas y las de México, particularmente en el tamaño de las hojas, tubo y lóbulos de la corola, frutos y semillas. Sin embargo, la forma de estas estructuras, son tan similares que no sugieren que los especímenes mexicanos pudieran corresponder a un taxón diferente, y por lo tanto asumimos que tales diferencias corresponden a variaciones propias de la especie.

Distribución y ecología.—En América, el género *Diodia* L. s. str., se encuentra ampliamente distribuido. De las cinco especies que se reconocen, tres restringen su distribución a Sudamérica, una se localiza en Cuba y Jamaica y otra se distribuye desde el SE de los Estados Unidos, México y Centroamérica (Bacigalupo y Cabral 1999). Para México se ha citado a *Diodia virginiana* y *Diodia maritima*, sin embargo los autores no han visto especímenes pertenecientes a tales especies, pero no se descarta su presencia. *Diodia saponariifolia* se encuentra ampliamente distribuida en la porción sureste del estado Veracruz y sólo se conoce de una localidad en el estado de Puebla. A pesar de la distancia tan amplia que separa dichas poblaciones de la especie, el hábitat es el mismo y corresponde a sitios húmedos, anegados o pantanosos. En México, estos sitios pueden estar colindando con distintos tipos de vegetación, como selvas altas perennifolias y pastizales inundados. Las selvas, prácticamente han sido sustituidas por vegetación secundaria o potreros que, sin embargo, aun cuentan con el hábitat característico de la especie. Tal condición fue confirmada por los autores al visitar la localidad de Bastonal a Santa Martha, donde la especie fue colectada por *A. Gómez Pompa & I. Calzada* (*5488*) en el año de 1978 en una porción de selva alta perennifolia y donde ahora solo hay restos de estas selvas pero se mantienen los suelos anegados donde vive la especie. Se distribuye desde los 0 hasta los 800 m de altitud, en suelos profundos, excepto en los suelos arenosos de la porción costera, que constituyen el hábitat natural de *Diodia maritima* en otras latitudes. La presencia de *Diodia saponariifolia* en México es un misterio, ya que en países de ubicación intermedia entre los extremos de distribución de la especie, cuyas floras han sido ampliamente estudiadas, como Costa Rica, Guatemala y Nicaragua (Burger & Taylor 1993; Standley & Williams 1975; Taylor 2001), no se conoce dicha especie. Una posible explicación puede deberse a su dispersión por aves migratorias que tienen preferencia por el hábitat pantanoso en su ruta migratoria, tal argumento ha sido utilizado por Thorne & Lathrop (1970) para explicar la distribución disyunta de *Pilularia americana* (Marsiliaceae).

AGRADECIMIENTOS

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CHRYSOTHAMNUS BAILEYI (ASTERACEAE) NUEVO PARA NUEVO LEÓN, MÉXICO

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RESUMEN

Se reporta a *Chrysothamnus baileyi* para el estado de Nuevo León. La distribución previamente conocida de la especie es del centro y sur de los Estados Unidos de América y noroeste de México. El nuevo registro extiende la distribución de la especie al sur en la región del Desierto Chihuahuense.

ABSTRACT

Chrysothamnus baileyi is reported for north central México (Nuevo León). It was previously known for the central and southern United States and northwestern Mexico. The new record extends the southward distribution of the species into the Chihuahuan Desert Region.

Durante la revisión de material botánico para el estado de Nuevo León, llamó la atención la presencia del género *Chrysothamnus* para la flora del estado, cuya existencia no había sido registrada previamente (Henrickson y Johnston 1997; Villarreal 2001). La especie al parecer es *C. baileyi* Wooton & Stand., la cual fue descrita en 1913 de un ejemplar colectado por *V.O. Bailey 498* en Nuevo Mexico. En 1923 fue transferido al siguiente nombre: *Chrysothamnus pulchelus* (A. Gray) Greene ssp. *bailey* (Wooton & Stand.) Hall & Clements, posteiormente en 1995 a *Ericameria pulchella* var. *bailey* (Wooton & Stand.) L.C. Anderson y recientemente en el 2005 a *Lorandersonia bailey* (Wooton & Stand.) Urbatsch, R.P. Roberts & Neubig.

Especimen de respaldo (voucher): **MÉXICO. Nuevo León. Municipio de Galeana:** S of Pablillo, ravine in mixed forest, 2203 m, 9 Oct 2009, *Hinton et al. 28939* (ANSM, herbario Hinton).

Otros ejemplares examinados: **MÉXICO. Nuevo León. Municipio de Galeana:** SW of Laguna de Labradores, arid gypsum hillside, 2264 m, 17 Oct 2009, *Hinton et al. 28021, 28102* (ANSM, TEX, herbario Hinton). Municipio de Doctor Arroyo, intersección of the Hwy 61 and the Hwy 3, 14.1 mi al S 100°28'24.96"W, 23°30'0.74"N, 26 Oct 1981, *Poole, Nixon & Smith 2508* (TEX).

La especie es un arbusto de 30–50 cm de alto que crece en matorrales y bosques de pino con *Pinus cembroides, Quercus intricata, Arctostaphylos pungens, Viguiera greggii, Chrysactinia mexicana, Helianthella gypsophila, Porophyllum filiforme, Dalea uniflora, Cheilanthes* spp., entre otras. Es poco común en el área y forma colonias esparcidas, creciendo también en suelos yesosos.

Chrysothamnus baileyi es conocido en los Estados Unidos de Arizona, Colorado, Kansas, Nuevo México, Oklahoma, Utah y de Trans-Pecos en Texas, y en México del noroeste-centro de Coahuila (Nesom in prep.; Urbatsch et al. 2005). Los nuevos reportes son del sur de Nuevo León por lo que la distribución conocida se extiende ahora hasta el sur de la región del Desierto Chihuahuense.

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ECOLOGÍA DEL BOSQUE DE *OSTRYA VIRGINIANA* (BETULACEAE) DE LA SIERRA DE ZAPALINAMÉ, COAHUILA, MÉXICO

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RESUMEN

Con el objetivo de conocer la estructura del bosque de *Ostrya virginiana* de la sierra de Zapalinamé se realizó un censo y se midió el diámetro a 1.30 m de alto de las especies arbóreas; además en el sitio se registraron: altitud, pendiente y datos del suelo. Se contabilizaron 115 árboles que pertenecen a cinco especies, con un diámetro promedio de 10 cm. *Ostrya virginiana* es la especie dominante, se censaron 108 árboles, los cuales tienen un área basal total de 0.827 m^2. Debido a la condición relictual del bosque se deberán implementar acciones de manejo para asegurar su conservación.

ABSTRACT

With the aim to know the structure of the *Ostrya virginiana* forest from the sierra de Zapaliname we made a census and measured the diameter breast height of the tree species, besides in the site were recorded: altitude, slope and soil data. There were 115 trees belonging to five species, with an average diameter of 10 cm. *Ostrya virginiana* is the dominant species, 108 trees were surveyed which have a total basal area of 0.827 m^2. Due to the relictual condition of the forest, management actions should be taken to ensure their conservation.

Ostrya virginiana K. Koch es un árbol caducifolio de 15 m o más de altura, con copa de forma piramidal, nativo de regiones templadas y húmedas de Norteamérica hasta zonas tropicales montañosas de Centroamérica (Islebe et al. 1994; Felger et al. 2001). Su distribución comprende amplios bosques en Canadá y el Este de Estados Unidos de América, donde forma parte del bosque deciduo templado o bosque de latifoliadas (Nixon et al. 1997). En México se distribuye en el bosque mesófilo de montaña, en los estados de Jalisco, Michoacán, Querétaro, Hidalgo, Veracruz, Guerrero y Chiapas (Rzedowski 1978, 1996), en la Sierra Madre Occidental se reporta para el suroeste de Durango (González et al. 2007), suroeste de Chihuahua y sureste de Sonora (Felger et al. 2001). En el noreste de México tiene distribución reducida y presenta bosques aislados (Valdez et al. 2003), en Tamaulipas se reporta para la sierra de San Carlos (Briones 1991) y la reserva de la Biósfera El Cielo (Puig et al. 1983); en Nuevo León se presenta en el centro-sur, en los municipios de Galeana, Santiago y Zaragoza (Hinton y Hinton 1995; Villarreal y Estrada 2008). Para el estado de Coahuila se tienen reportes de colecta en las sierras del Carmen, Santa Rosa y La Gloria, ubicadas en el centro-norte de la entidad (Villarreal 2001). Actualmente *Ostrya virginiana* es una especie listada en estatus de conservación según la Norma oficial mexicana NOM-059-SEMARNAT-2010 (SEMARNAT 2010), bajo la categoría de Sujeta a protección especial; sin embargo, su distribución ha sido afectada de manera importante por la tala inmoderada y la destrucción del hábitat con fines agrícolas y ganaderos (Luna 2003); a pesar de ello se carece de estudios enfocados a conocer el estado actual de sus poblaciones que permitan establecer las estrategias más adecuadas para su conservación a largo plazo en el país. La Sierra de Zapalinamé es un área natural protegida bajo la categoría de Zona Sujeta a Conservación Ecológica, decretada por el gobierno del estado de Coahuila (Anónimo 1996). Se pretende estudiar la estructura y ecología del bosque de *Ostrya virginiana* de la Sierra de Zapalinamé y con ello promover su conservación.

ÁREA DE ESTUDIO

La sierra de Zapalinamé se localiza en el sureste de Coahuila, en los municipios de Saltillo y Arteaga; es una zona de transición entre el Desierto Chihuahuense y la Sierra Madre Oriental. Se ubica entre los 25°15'00" - 25°25'58.35" de latitud Norte y entre 100°47'14.5" - 101°05'3.8" de longitud Oeste (Fig. 1). Pertenece a la

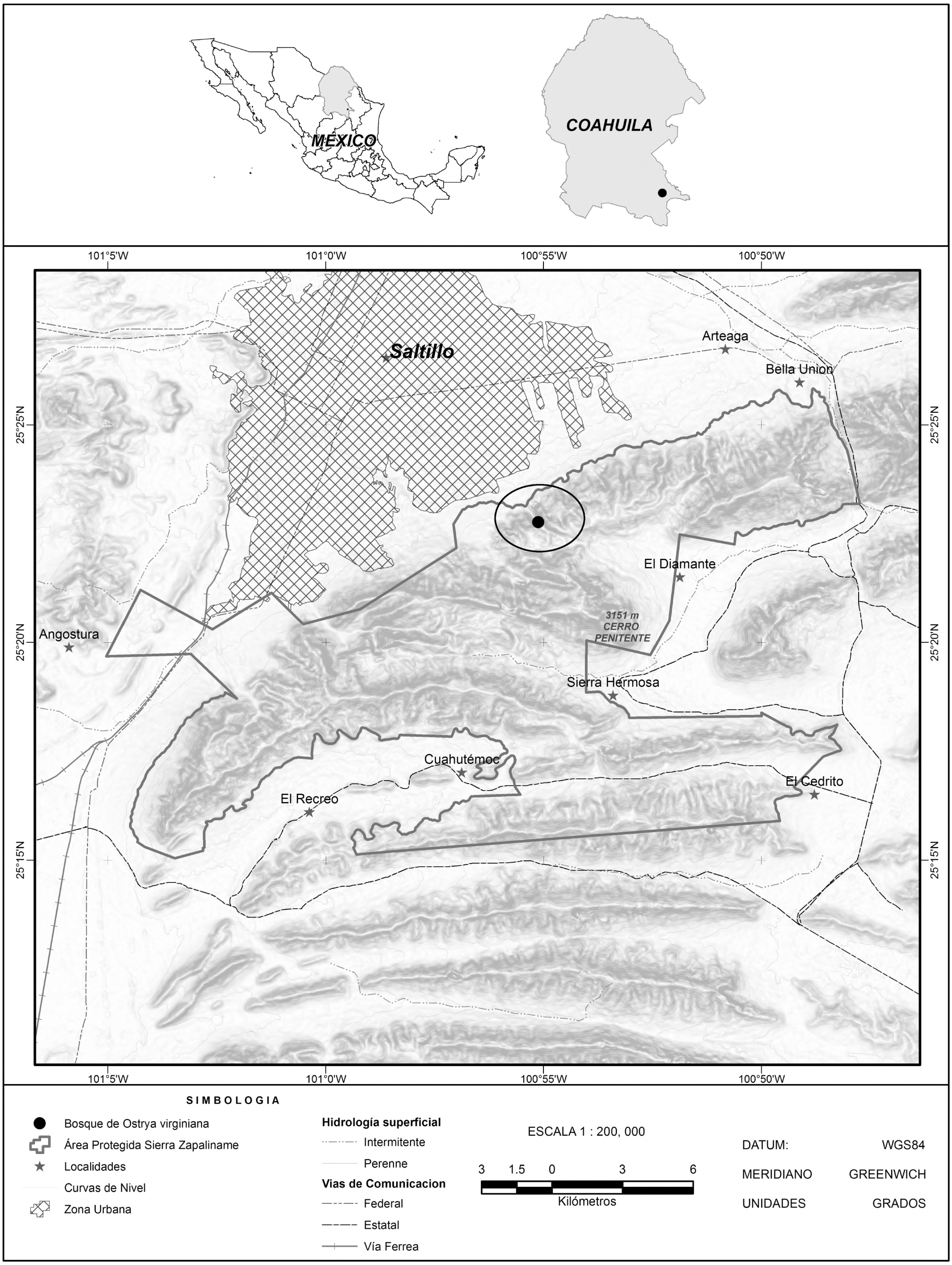

Fig. 1. Distribución de *Ostrya virginiana* en la Sierra de Zapalinamé.

subprovincia de la Gran Sierra Plegada (Anónimo 1998), con altitudes entre 1,590 a 2,200 m, alcanza su mayor elevación a 3,140 m en El Penitente. Las rocas son sedimentarias marinas del Jurásico y Cretácico, las calizas ocupan 43% del área. Los suelos dominantes son litosol y rendzina. El área tiene un clima BSokw"(e), seco, templado, extremoso en las partes bajas de la zona y templado C(wo) en las altas, hacia la parte sur de la sierra el clima es semiárido y subhúmedo en el sureste, la temperatura media anual es de 18ºC. La precipitación promedio es 498 mm, de tipo convectivo y ocurre en verano (Anónimo 1998). En áreas con exposición sur se presenta matorral rosetófilo, en laderas bajas de exposición norte crece el matorral submontano de rosáceas, mientras que en cañones con más humedad bosques de encino y en las partes altas crecen bosques de pino y oyamel (Marroquín 1976; Arce y Marroquín 1985).

METODOLOGÍA

Se realizó un censo de las especies arbóreas presentes en el bosque de *Ostrya virginiana*, a cada árbol se le midió el diámetro normal (a 1.30 m) y la altura total. Se listaron las especies que integran los estratos arbustivo y herbáceo. Se registró altitud (tomada de un altímetro-barómetro), coordenadas geográficas (con un GPS), pendiente (mediante una pistola Haga) y exposición topográfica (tomada con una brújula), además de registrar las propiedades físicas del suelo. Se recolectaron muestras botánicas que posteriormente se herborizaron, identificaron e incluyeron en el herbario ANSM (Holmgren et al. 1990). La estructura horizontal se analizó en términos del área basal y la densidad de árboles por categorías diamétricas, con los valores relativos de ambos atributos se calculó el índice de dominancia relativa por especie (en lo sucesivo IDR) (Mueller y Ellemberg 1974).

RESULTADOS

El bosque de *Ostrya virginiana* se localiza en el fondo del cañón Los Pericos, del ejido San José de los Cerritos (25°22'46"N - 100°55'07"W), donde hay mayores condiciones de humedad, éste se ubica en la exposición noroeste de la sierra, también conocida como ¨El Frente¨, a una altitud de 2,200 m, el clima es seco templado con verano cálido extremoso BSok(x')(e), la temperatura media anual es 12 a 16°C y la precipitación de 450 y 550 mm, el sustrato geológico está formado por rocas sedimentarias, los suelos son de tipo rendzina, pedregosos y alcalinos, con bajo contenido de materia orgánica y profundidad inferior a 20 cm, la pendiente del terreno es superior al 70%.

Como parte del bosque se cuantificaron 115 árboles que pertenecen a cinco especies, con alturas de 2 hasta 10 m y diámetro promedio de 10 cm. La especie con la mayor contribución a la estructura (93.31% del IDR) es *Ostrya virginiana*, de la cual se censaron 108 individuos, con un área basal total de 0.827 m^2 (Tabla 1); además se registraron otros árboles como: *Celtis laevigata* Willd., *Fraxinus cuspidata* Torr., *Cercis canadensis* L. var. *mexicana* (Rose) Hopk. y *Sideroxylon lanuginosum* Michx. subsp. *rigidum* (A. Gray) T.D. Pennington, los cuales crecen dispersos a través del bosque y presentan una densidad total de 7 individuos y un área basal de 0.064 m^2. El estrato arbustivo está dominado por individuos aislados de *Sideroxylon lanuginosum* subsp. *rigidum*, por su parte, en el herbáceo las especies más comunes son: *Sedum wrightii* A. Gray ssp. *priscum* Clausen, *Tradescantia pringlei* S. Watson, *Stachys bigelovii* A. Gray y *Salvia grahamii* Benth., de manera aislada se presentan *Dahlia coccinea* Cav. y *Bromus carinatus* Hook. et Arn. La especie trepadora *Parthenocissus quinquefolia* (L.) Planch., es abundante sobre troncos de los árboles y en rocas expuestas.

La distribución diamétrica del bosque se presenta en la Figura 2, donde se observa que está estructurado en ocho categorías diamétricas. La categoría con mayor densidad es la menor a 5 cm de diámetro con 62 árboles de *Ostrya virginiana* (que representan el 66% del total), seguida por la de 5 cm con 17. El número de árboles de las categorías diamétricas mayores es drásticamente menor, de ésta forma las de 25, 30 y 40 cm solo presentan un individuo, mientras que en la de 35 cm, no se presentaron arboles. Las otras especies arbóreas: *Celtis laevigata*, *Fraxinus cuspidata*, *Cercis canadensis* presentan 1 individuo cada una, mientras que de *Sideroxylon lanuginosum* subsp. *rigidum* se registraron 4 árboles, todas distribuidas en las primeras cinco categorías.

Tabla 1. Atributos estructurales del estrato arbóreo del bosque de *Ostrya virginiana* de la Sierra de Zapalinamé.

Especie	Densidad total	Densidad relativa (%)	Área basal total (m^2)	Área basal relativa (%)	IDR (%)*
Ostrya virginiana	108	93,91	0,827	92,71	93,31
Celtis laevigata	1	0,86	0,031	3,52	2,19
Sideroxylon lanuginosum subsp. *rigidum*	4	3,47	0,006	0,73	2,10
Fraxinus cuspidata	1	0,86	0,019	2,13	1,49
Cercis canadensis var. *mexicana*	1	0,86	0,008	0,89	0,88
Total	115	100	0,892	100	100

* IDR = Índice de dominancia relativa.

DISCUSIÓN

En el estado de Coahuila el bosque deciduo templado (Marroquín 1976) es una comunidad relictual que se restringe a cañones de algunas áreas montañosas del centro-norte de la entidad (Muller 1947; Wood et al. 1999; Henrickson y Johnston 2004) y que en el terciario formaron bosques abundantes (Axelord 1975), los cuales, debido a cambios climáticos y geomorfológicos durante el Plioceno y el Pleistoceno redujeron su distribución a las zonas más húmedas (Gentry 1982; Toledo 1982). Por lo anterior, la presencia de *Ostrya virginiana* para la Sierra de Zapalinamé es de relevancia, ya que por su ubicación en la transición entre la Sierra Madre Oriental y el Desierto Chihuahuense (Anónimo 1998) el clima seco-templado domina en el área y contrasta con el centro y este de México, donde el clima es húmedo-templado y es más frecuente el bosque mesófilo de montaña (Rzedowski 1978; Carranza y Madrigal 1995; Luna 2003), comunidad vegetal de la cual forma parte ésta especie, lo anterior, le confiere una condición de rareza en la vegetación de la serranía.

El bosque estudiado se distribuye a 2,200 m de altitud, por lo cual se ubica dentro del gradiente altitudinal de *Ostrya virginana* reportado para México que va de 1,200 a 2,800 m (Luna 2003) y es superior a la reportada para los bosques del centro-sur de Nuevo León (Hinton y Hinton 1995) que corresponden a 2,095 y 2,165 m en los municipios de Galeana y Zaragoza, respectivamente. Debido a que en la Sierra de Zapalinamé prevalecen condiciones climáticas xéricas para el desarrollo de *Ostrya virginiana*, la altura de los arboles y el diámetro de los troncos son menores a los reportados para la especie en el bosque mesófilo de México, donde éstos presentan alturas dos veces mayores y diámetros que exceden hasta tres veces el promedio registrado (Jardel et al. 1996; Alcántara y Luna 2001; Ponce et al. 2006). Sin embargo, a pesar de la baja precipitación en el área, el análisis estructural mostró una mayor densidad de individuos con diámetros ≤5 cm, los cuales, de acuerdo a Encina et al. (2009) se clasifican como renuevos y juveniles, esto señala que la especie tiene buena regeneración y que es una población joven en vías de crecimiento (Kormondy 1985). Existen factores que amenazan la permanencia de este bosque, como los incendios forestales que ocurren con frecuencia en la sierra, esto debido a la cercanía con la ciudad de Saltillo, por lo cual el bosque es susceptible de ser dañado, además, por la ubicación en un talud, algunos árboles presentan raíces expuestas, ante esto se recomienda implementar técnicas de conservación de suelos para lograr su retención. Debido a la condición relictual de ésta especie para el macizo montañoso, se deberá realizar la colecta de germoplasma y fomentar su establecimiento en el mismo cañón o en sitios con condiciones ecológicas similares y considerando que uno de los objetivos del área protegida ¨Sierra de Zapalinamé¨ es la conservación de la biodiversidad, sobre todo de las especies vulnerables (Anónimo. 1998), se podría asegurar su conservación a largo plazo.

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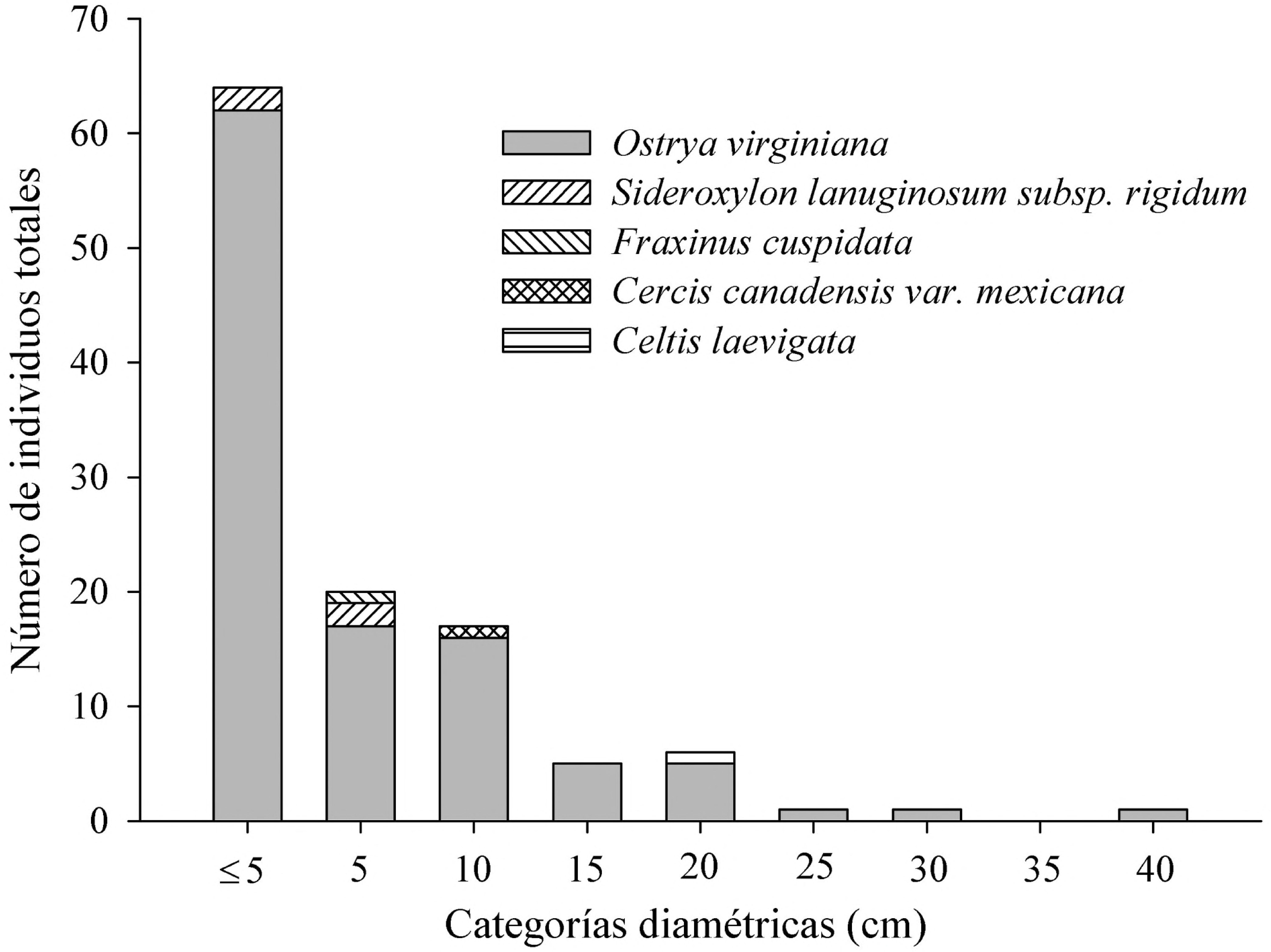

Fig. 2. Estructura diamétrica de las especies arboreas del bosque de *Ostrya virginiana* en la Sierra de Zapalinamé.

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BEE FLORA OF AN INSULAR ECOSYSTEM IN SOUTHERN BRAZIL

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ABSTRACT

The present work aims to catalogue the diversity of plants visited by bees in the Floresta and Laranjeira islands within a preservation area in the floodplain of the Paraná River. Monthly field trips were conducted from August 2005 to July 2006 to collect plant species visited by *Apis mellifera*. A total of 521 plant samples were collected and identified, resulting in a list of 135 species distributed among 53 families and 104 genera. The most important families were Asteraceae (15), Rubiaceae (10), Fabaceae (7), and Solanaceae (6). Based on the number of diverse plant utilized by *A. mellifera,* it is clear that their diversity is important for beekeepers in the tropical Americas.

Key Words: *Apis mellifera*, Paraná River, pollination, floral traits

RESUMEN

Este estudio tuvo como objetivo contribuir al conocimiento de la diversidad de las especies visitadas por abejas en las islas de Laranjeira y Floresta, una área de conservación en la zona de inundación del río Paraná. El muestreo se llevo a cabo mensualmente de agosto 2005 a julio 2006 con especies de plantas visitadas por *Apis mellifera*. Un total de 521 muestras de plantas visitadas por *Apis mellifera* fueron recogidas e identificadas. Se encontraran 135 especies pertenecientes a 104 géneros y 53 familias. Las familias con mayor número de especies son Asteraceae (15), Rubiaceae (10), Fabaceae (7) y Solanaceae (6). Como un número considerable de especies de la Flora de las Islas esta asociada a la presencia de *A. mellifera*, esas especies son claramente importantes para los apicultores de la América tropical.

INTRODUCTION

Insects, especially bees, comprise one of the main groups of angiosperm pollinators, and, as such, they play a vital role in the biology of plant communities, being mainly responsible for gene flow among individuals and populations. From this perspective, considerable research is in progress to increase the knowledge about bee flora and its interaction with the pollinators (Rodarte et al. 2008; Mendonça et al. 2008; Vieira et al. 2008). The diversity of Brazilian flora, given the territorial extension and climatic variability of the country, greatly influences the potential of beekeeping (Marchini et al. 2004).

Bee flora is defined by the number of plant species that bees use as a source of nectar and pollen for

their survival and production of honey (Pereira 1990). While bee flora in Brazil is rich and varied, there is still insufficient information on beekeeping and the plants used by honey bees. Most data available come from studies from temperate zones (Almeida-Anacleto 2007). Identification of plant species visited by bees is important for beekeepers because such information can optimize honey production through the use of appropriate sources of nectar and pollen (Alcoforado-Filho 1993). Furthermore, knowing the floral source of honey enables beekeepers to characterize their products (Almeida-Anacleto 2007). The pollen found in honey is an indicator of its botanical origin and, through quantitative analysis, it is possible to establish the relative contribution of each plant to honey production (Iwama & Melhem 1979). Knowledge of the botanical and geographical origin of pollen sources (Almeida-Anacleto 2007) is used in this type of analysis, and it is also a requirement of the international quality control of honey.

Brazilian apiculture has been steadily growing, and it is internationally renowned for its control methods of Africanized honey bees, as well as the large diversity and quality of its manufacturing products (centrifuge, tanks, cylinders to produce molded wax, and bee hives), and the production, mainly organic, of such bee products as honey, pollen, royal jelly and propolis. For those reasons, Brazil has potential for the production of organic honey, which, if properly certified, can be competitive in the international market (Buainin & Batalha 2007). There are several projects for the production of organic honey now underway in the country. In Paraná State, for example, it is estimated that more than nine thousand certified beehives exist, with an average annual production of 400,000 kg of organic honey by 75 beekeepers. It is estimated that the islands of the upper and middle Paraná River have more than 15,000 productive hives. World production of honey by the 15 major producing countries grew 30.15% from 1994 to 2005. Over the last ten years, Brazil has been the country with the largest expansion of honey exports, both in value and quantity. In 2006, the production reached 38 thousand tons, representing R$ 120 million. (IBGE 2009).

The Laranjeiras and Floresta Islands are located in a protected area of the upper Paraná River floodplain. The southern region of the area can be considered the last remnant of "varzeas" in the Paraná River, free of dams (Campos 2001). Several floristic and phytosociological studies have been carried out in the area, (e.g., Campos et al. 2000; Campos & Souza 2003). The basis for consolidated beekeeping depends on sound information about local flora and its phenology, as well as the determination of apiculture potential (Silveira 1983).

This study aimed to identify the plants visited by bees in a protected area of the Paraná River, which is known as the Parque Nacional da Ilha Grande, and characterize them, taking into account the floral morphology, to provide better information for the management of bee colonies in the studied area.

The Ilha Grande National Park (PNIG) is a Unity of Conservation for Integral Protection. It covers approximately 78,878 ha of semideciduous forests at the borders of Paraná and Mato Grosso do Sul States in Brazil (IBGE 1992). The study area is located in the PNIG and is bounded by the Laranjeira and Floresta islands near the municipality of Querência do Norte (22°55'00"S, 53°35'00"W and 22°48'00"S, 53°25'00"W, respectively). The region is dominated by lakes, ponds and about 300 islands (Campos 2001). Since this region contains the Biodiversity Corridor of the Paraná River, it is important for the conservation of the natural resources present in the area. Most of the original vegetation was destroyed, giving way to coffee plantations and cattle fields. The park protects the last stretch of the Paraná River free of dams in Brazil. For those reasons, the PNIG is internationally recognized as a core area of the Biosphere Reserve of the Atlantic Forest (MaB Programme of UNESCO). The park protects areas used by migratory birds and rare species, as well as both endemic and endangered flora and fauna. The area also provides several types of economic activity for the local population. Particularly important to this work, it is estimated that there are about 10,000 bee boxes within the park, according to beekeepers of Paraná. This activity has generated additional income for local residents, and it has grown in importance in a regional economic context.

MATERIAL AND METHODS

The collection sites at Laranjeira and Floresta islands are indicated in Figure 1. The climate of the region,

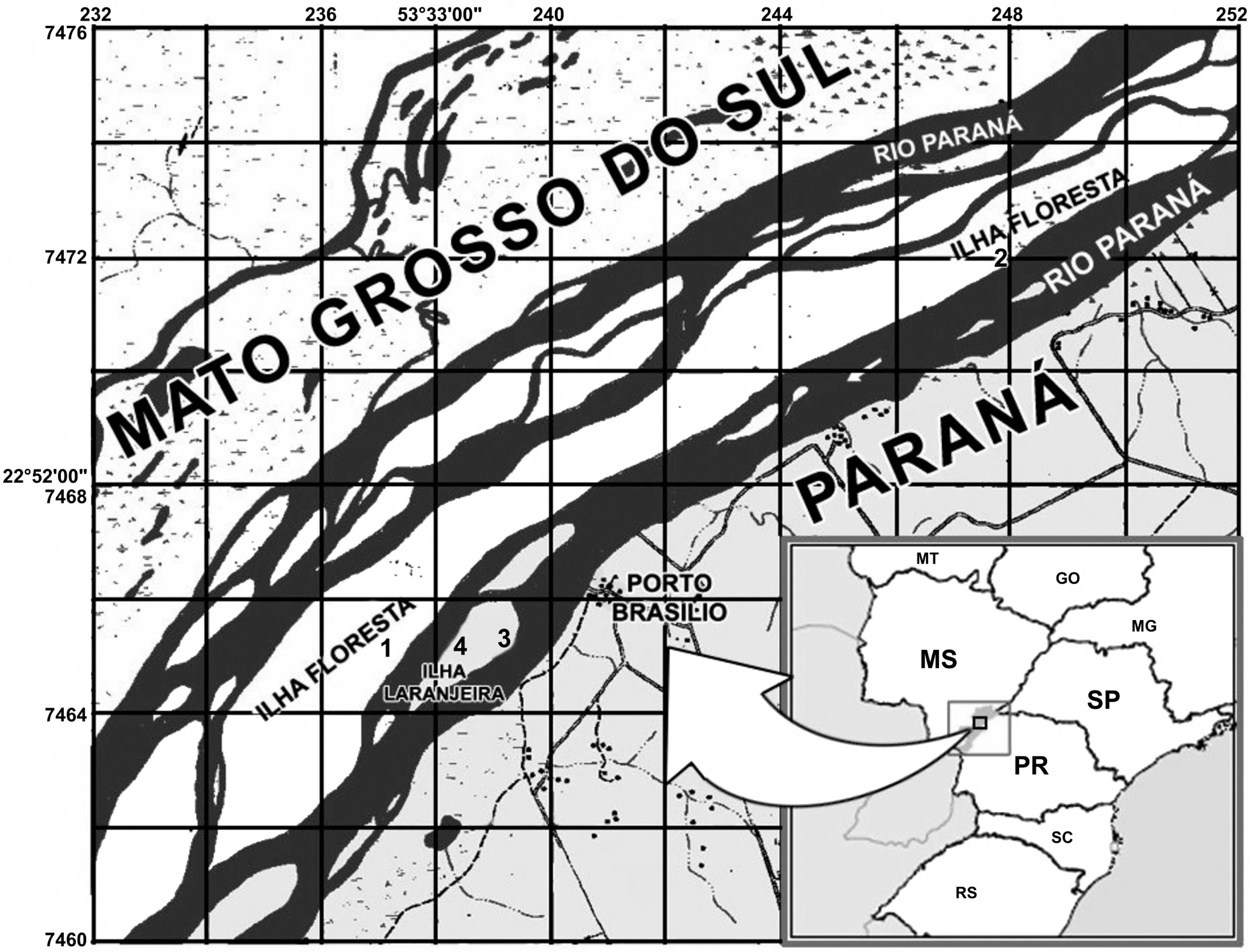

Fig. 1. Map of the study area. Numbers 1–4 indicate the points of transversal pathways in the Laranjeiras and Floresta islands where the collections were made.

according to the classification of Köppen, is type Cfa – humid, subtropical (Maak 1968). The rainfall is distributed throughout the year, with higher precipitations from September to December and a drier season from June to August (Caviglione et al. 2000).

The samples were collected monthly, between August 2005 and August 2006. Trails (12 for Laranjeira Island and 10 for Floresta Island) were established throughout the study area, especially near the apiaries. A plant was considered visited by *Apis melifera* only when the bee was found within its flowers. All plants visited by *Apis mellifera* were collected. In the field, notes were taken to describe the color and symmetry of the flowers. In the laboratory, the symmetry of all corollas was reanalyzed and classified as actinomorphic, zygomorphic or asymmetric (Bell 2008).

All fertile material was collected according to the standard botanical procedures (Bononi et al. 1984; Liesner 2010). Specimens were deposited into HUEM and identified using specific literature and comparison with collections held at RB and FUEL (acronyms follow Holmgren et al. 1990). Whenever necessary, taxonomy specialists were also consulted. Duplicates were sent to RB. The organization of families followed APG II (2003).

RESULTS AND DISCUSSION

The studied area presents a high degree of deforestation as a consequence of its use for pasture land and fires that have occurred throughout the last three decades (Campos & Souza 2003). Between 1999 and 2003,

52 fires were documented in the IGNP, and most of them reached meadow areas and fragments of seasonal semideciduous forest (Abreu et al. 2004). During the development of this study, part of Laranjeira Island was also struck by fire in September, 2005. In spite of both fire damage and deforestation, plant species visited by bees were found in all habitats: gallery forest, meadow, paludiculous and aquatic (terminology for riparian formations according to Souza & Kitta 2007). Several species were typical of seasonal semideciduous submontane vegetation, possibly indicating a reasonable degree of preservation of local flora: *Guarea macrophylla* Lam., *Trichilia pallida* Sw. (Meliaceae), *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae), *Crysophyllum lucentifolium* Cronq. (Sapotaceae), *Nectandra cissiflora* Ness, *Ocotea langsdorffii* (Meiss.) Mez (Lauraceae), *Eugenia punicifolia* Kunth (DC) (Myrtaceae) and *Inga sessilis* (Vell.) Mart. (Fabaceae). On the other hand, other species were considered invasive plants, evidencing the impact of human activities in the islands. Species of *Vernonia*, *Eupatorium*, *Croton* and *Ipomoea* have frequently been cited in the literature as invasive, but also as apiculous plants. *Vernonanthura phosphorica* (Vell.) H. Rob. (Asteraceae), *Lantana trifolia* (Verbenaceae) and *Crotalaria micans* (Fabaceae) have all been considered as important bee plants (Lorenzi 2000). *V. phosphorica* and some species of *Mikania* were listed in the Directory of Important World Sources, confirming the importance of the family Asteraceae among the families visited by bees.

Pfaffia glomerata (Amaranthaceae), one of the visited species, is sometimes considered as invasive as well as an important medicinal plant found in the area. Since it is also one of the first species to appear in areas affected by fire, it is considered ecologically important as a pioneer species (Taschetto & Pagliarini 2003).

This study found 135 bee-visited species distributed among 104 genera and 53 families in the area (Table 1). Besides the importance for beekeepers, this information is also useful for plant ecology studies, since bee-visiting can be a good proxy for pollination. For example, Freitas and Sazima (2006) verified that *Apis mellifera* was responsible for pollinating 31 out of 124 bee-visiting species. Using the number of species as a metric, the most important families were Asteraceae (15), Rubiaceae (10), Fabaceae (7) and Solanaceae (6). The genera with highest species richness were *Ludwigia* and *Solanum*, both with four species. *Ipomoea, Croton, Passiflora, Gouania* and *Psycothria* presented three species each. Asteraceae, Myrtaceae, Rubiaceae, Euphorbiaceae and Lamiaceae are the most important botanical families for *A. mellifera* in the neotropics (Ramalho et al. 1990). Locatelli and Machado (2001) pointed out the importance of Asteraceae as a particularly rich family of plant species visited by bees. They suggested that the great number of species and the wide geographical distribution of the family favor this fact.

Comparatively, the Fabaceae, one of the most diverse families in the studied area, was highly represented (seven species) in the bee flora of a sandbank area in Bahia, northeastern Brazil (Viana et al. 2006). This family was also among those with the largest number of species (14) visited by bee species in a transition area among seasonal deciduous forest, savanna and ombrofilous forest in Castro Alves, Bahia (Carvalho & Marchini 1999).

Although the studied area was near Maringá (about 250 km), the results of the present study are very different from those of Toledo et al. (2003). These authors found that Anacardiaceae and Sterculiaceae were the most visited families by *Apis mellifera* in Maringá, probably reflecting the choice of an urban environment for their bee flora study.

With respect to pollen, geographical distribution of plants and honey production, the pollen of *Allophyllus* (Sapindaceae) and *Casearia* (Salicaceae) was considered by Ramalho et al. (1991) to be a good geographical indicator of honey collected in southern Brazil. The genera were considered an important honey source for that region and important for beekeepers in the tropical Americas.

Only *Maranta divaricata* was considered asymmetrical, while the remaining visited plants presented actinomorphic (83%) and zygomorphic flowers (17%). In the study of Freitas and Sazima (2006) involving 124 species, radial symmetry (actinomorphic flowers) occurred in 69% of the flowers versus 26% of flowers with bilateral symmetry (zygomorphic flowers). According to Zoucas et al. (2004), *Apis mellifera* prefers actinomorphic flowers. Since our study concluded that the majority of plants in the study area presented

Table 1. Plants visited by *Apis mellifera* in the Laranjeiras and Floresta Islands. **Hab** – Habit, **Infl** – Inflorescence, **HUEM** (registration number in the Herbarium of the University of Maringá), **HER**- Herb, **SUB**- Subshrub, **SBR**- shrub, **CRE**- Climber or Liana, **TRE**- Tree, **ACT**- Actinomorphic flower, **ZIG**- Zygomorphic flower, **ASY** – Asymmetrical flower, **RED**- Red, **WHI**- White, **CRE**- Cream, **YEL**- Yellow, **ORA**- Orange, **PUR**- Purple, **PIN**- Pink, **VIN**- Vinaceous.

Species	Family	Hab.	Corolla	HUEM	Color
Justicia brasiliana Roth	Acanthaceae	SUB	ZIG	12794	RED
Ruellia angustifolia (Ness.) Lindau	Acanthaceae	SUB	ZIG	12305	RED
Echinodorus grandiflorus (Cham & Schltdl.) Micheli	Alismataceae	HER	ACT	12306	WHI
Alternathera philoxeroides (Mart.) Griseb.	Amaranthaceae	SUB	ACT	12313	WHI
Chamissoa altissima (Jacq.) Kunth	Amaranthaceae	SUB	ACT	12820	CRE
Chamissoa macrocarpa (Kunth)	Amaranthaceae	SUB	ACT	12579	WHI
Pfaffia glomerata (Spreng.) Pedesen	Amaranthaceae	SUB	ACT	12311	WHI
Pfaffia paniculata (Mart.) Kuntze	Amaranthaceae	SUB	ACT	12309	WHI
Guatteria campestris R.E. Fr	Annonaceae	TRE	ACT	12589	CRE
Rollinia emarginata Schltdl.	Annonaceae	TRE	ACT	12573	YEL
Asclepias curassavica L.	Apocynaceae	HER	ACT	12329	ORA
Oxypetalum cordifolium (Vent.) Schltdl.	Apocynaceae	CRE	ACT	12858	CRE
Prestonia coalita (Vell.) Woodson	Apocynaceae	CRE	ACT	12582	YEL
Tabermontana catharinensis A. DC.	Apocynaceae	TRE	ACT	12323	WHI
Aristolochia cymbifera Marrt. & Zucc	Aristolochiaceae	CRE	ZIG	12328	PUR
Achyrocline saturejoides (Lam.) D.C.	Asteraceae	SUB	ACT	12559	YEL
Ageratum conyzoides L.	Asteraceae	SUB	ACT	12228	PUR
Conyza bonariensis (L.) Cronq.	Asteraceae	SUB	ACT	12556	CRE
Chromolaena laevigata (Lam) R.M. King & H. Rob.	Asteraceae	SBR	ACT	12216	PIN
Cosmos sulphureus Cav.	Asteraceae	SUB	ACT	12237	YEL
Mikania micrantha Kunth	Asteraceae	CRE	ACT	12232	WHI
Mikania officinalis Mart.	Asteraceae	CRE	ACT	12767	WHI
Pluchea sagittalis (Lam.) Cabrera	Asteraceae	TRE	ACT	12556	YEL/PIN
Porophyllum ruderale (Jacq.) Cass.	Asteraceae	SUB	ACT	12229	CRE
Schkuhria pinnata (Lam.) Kuntze	Asteraceae	SUB	ACT	12236	CRE
Verbesina encelioides (Cav.) H. & B.	Asteraceae	SUB	ACT	12219	YEL
Vernonanthura phosphorica (Vell.) H. Rob.	Asteraceae	SBR	ACT	12217	WHI
Chrysolaena platensis (Spreng.) H.Rob.	Asteraceae	SBR	ACT	12557	CRE/PIN
Vernonia echioides Less.	Asteraceae	SBR	ACT	12208	WHI
Begonia sp.	Begoniaceae	HER	ACT	12331	PIN
Arrabidaea patellifera (Schltdl.) Sandwith	Bignoniaceae	CRE	ZIG	12332	PUR
Arrabidaea chica (Humb. & Bonpl.) B. Verl.	Bignoniaceae	CRE	ZIG	12875	PIN
Cordia sellowiana Cham.	Boraginaceae	SBR	ACT	12334	WHI
Heliotropium cf. *angiospermum* Murray	Boraginaceae	CRE	ACT	12336	WHI
Heliotropium transalpinum Vell.	Boraginaceae	HER	ACT	12333	WHI
Protium heptaphyllum Marchand	Burserceae	TRE	ACT	12569	CRE
Trema micrantha (L.) Blume	Cannabaceae	TRE	ACT	12860	WHI
Cheiloclinium cf. *cognatum* (Miers.) A.C. Sm.	Celastraceae	CRE	ACT	12734	CRE
Combretum fruticosum (Loefl.) Stuntz	Combretaceae	CRE	ACT	12397	YEL
Commelina erecta L.	Commelinaceae	HER	ZIG	12337	PUR
Ipomoea cairica (L.) Sweet	Convolvulaceae	CRE	ACT	12346	PIN
Ipomoea cf. *carnea* Jacq.	Convolvulaceae	CRE	ACT	12344	PIN
Ipomoea tiliacea (Willd.) Choisy	Convolvulaceae	CRE	ACT	12339	PIN
Merremia digitata (Spreng.) Hallier f.	Convolvulaceae	CRE	ACT	12342	WHI
Doliocarpus dentatus (Aubl.) Standl.	Dilleniaceae	CRE	ACT	12430	RED/YEL
Tetracera breyniana Schlech.	Dilleniaceae	CRE	ACT	12798	YEL
Sloanea guianensis Benth	Elaeocarpaceae	TRE	ACT	12354	CRE
Erythroxylum pulchrum A. St.-Hil	Erythroxylaceae	TRE	ACT	12760	WHI
Croton cf. *glandulosus* L.	Euphorbiaceae	SCR	ACT	12373	CRE
Croton floribundus Baill.	Euphorbiaceae	TRE	ACT	12385	CRE
Croton urucurana Baill.	Euphorbiaceae	TRE	ACT	12377	CRE
Dalechampia brasiliensis Lam.	Euphorbiaceae	CRE	ZIG	12360	CRE/RED

Table 1. continued

Species	Family	Hab.	Corolla	HUEM	Color
Phyllanthus tenellus Roxb.	Phyllanthaceae	SUB	ACT	12362	CRE/RED
Desmodium sp.	Fabaceae (Pap.)	SBR	ZIG	12846	PIN
Dioclea grandiflora Mart. ex Benth.	Fabaceae (Pap.)	SBR	ZIG	12744	PUR
Inga sessilis (Vell.) Mart. ex Benth	Fabaceae (Mim.)	TRE	ACT	12834	WHI
Mimosa micropteris (Burk.) Barneby	Fabaceae (Mim.)	SBR	ACT	12845	PIN
Aeschynomene sensitiva Sw.	Fabaceae (Pap.)	SUB	ZIG	12867	YEL
Chaetocalyx scandens (L.) Urb.	Fabaceae (Pap.)	CRE	ZIG	12849	YEL
Crotalaria micans Link.	Fabaceae (Pap.)	SUB	ZIG	12837	YEL
Heliconia laneana Barreiros	Heliconiaceae	HER	ZIG	12262	RED
Hyppericum sp.	Hyppericaceae	HER	ACT	12882	YEL
Aegiphila sellowiana Cham.	Lamiaceae	SUB	ZIG	12426	WHI
Aegiphilla sp.	Lamiaceae	CRE	ZIG	12752	YEL
Nectandra cissiflora Nees	Lauraceae	TRE	ACT	12799	WHI
Ocotea langsdorffii (Meiss.) Mez	Lauraceae	TRE	ACT	12826	WHI
Cuphea melvilla Lindl.	Lythraceae	SUB	ZIG	12853	PIN
Cuphea calophylla Cham. & Schltdl.	Lythraceae	SUB	ZIG	12852	PIN
Mascagnia affinis W.R. Anders. & C.C. Davis	Malpighiaceae	CRE	ACT	12247	PIN
Luehea cf. *divaricata* Mart.	Malvaceae	TRE	ACT	12412	PIN
Sida rhombifolia L.	Malvaceae	SUB	ACT	12252	CRE
Maranta divaricata Roscoe	Marantaceae	HER	ASY	12537	WHI
Clidemia hirta (L.) D. Don	Melastomataceae	SBR	ACT	12257	WHI
Miconia staminea (Desr.) DC.	Melastomataceae	SBR	ACT	12256	WHI
Tibouchina sebastianopolitana (Raddi) Cogn.	Melastomataceae	TRE	ACT	12258	LIL
Guarea macrophylla Lam.	Meliaceae	TRE	ACT	12266	CRE
Trichilia pallida Sw.	Meliaceae	TRE	ACT	12791	CRE
Trichillia elegans A. Juss.	Meliaceae	TRE	ACT	12757	CRE
Eugenia cf. *neoverrucosa* Sobral	Myrtaceae	SBR	ACT	12260	CRE
Eugenia punicifolia (Kunth) DC.	Myrtaceae	SBR	ACT	12812	WHI
Myrcia sp.	Myrtaceae	TRE	ACT	12259	CRE
Syzygium jambolanum DC.	Myrtaceae	SBR	ACT	12587	YEL
Pisonia ambígua Heimeri	Nyctaginaceae	CRE	ACT	12769	CRE
Ludwigia hookeri (Micheli) H. Hara	Onagraceae	HER	ACT	12516	YEL
Ludwigia leptocarpa (Nutt.) H. Hara	Onagraceae	HER	ACT	12511	YEL
Ludwigia octovalvis (Jacq.) Raven	Onagraceae	HER	ACT	12522	YEL
Ludwigia uruguayensis (Cambessa) H. Hara	Onagraceae	HER	ACT	12520	YEL
Passiflora foetida L.	Passifloraceae	CRE	ACT	12349	WHI
Passiflora misera H.B.K.	Passifloraceae	CRE	ACT	12864	WHI
Passiflora alata Curtis	Passifloraceae	CRE	ACT	12528	WHI
Picramnia sellowii Planch.	Picramniaceae	SBR	ACT	12756	YEL
Piper umbellatum L.	Piperaceae	SBR	ACT	12531	CRE
Piper sp.	Piperaceae	SBR	ACT	12534	CRE
Angelonia integerrima Spreng.	Plantaginaceae	HER	ACT	12739	PIN
Polygonum acuminatum H.B.K.	Polygonaceae	HER	ACT	12543	PIN
Polygonum punctatum (Meiss.) Small	Polygonaceae	HER	ACT	12542	CRE
Triplaris americana L.	Polygonaceae	TRE	ACT	12539	PIN/CRE
Eichornea crassipes (Mart.) Solms.	Pontederiaceae	HER	ZIG	12546	LIL
Pontederia cordata Nutt.	Pontederiaceae	HER	ZIG	12547	LIL/YEL
Gouania latifolia Reissek	Rhamnaceae	CRE	ACT	12821	CRE
Gouania mollis Reissek	Rhamnaceae	CRE	ACT	12580	CRE
Gouania virgata Reissek	Rhamnaceae	CRE	ACT	12365	WHI
Borreria cf. *capitata* (Ruiz & Pavon) DC.	Rubiaceae	SUB	ACT	12453	WHI
Cephalanthus glabratus Schum.	Rubiaceae	SUB	ACT	12288	WHI
Diodia gymnocephala (DC) Schum.	Rubiaceae	SUB	ACT	12450	WHI
Diodia sarmentosa Sw.	Rubiaceae	SUB	ACT	12285	WHI

Table 1. continued

Species	Family	Hab.	Corolla	HUEM	Color
Gallianthe brasiliensis (Spreng.) E. Cabral & Bacigalupo	Rubiaceae	SUB	ACT	12452	WHI
Machaonia brasiliensis Cham. & Schltdl.	Rubiaceae	SBR	ACT	12289	WHI
Palicourea marcgravii St. Hil.	Rubiaceae	SBR	ACT	12300	YEL/PIN
Psychotria barbiflora DC.	Rubiaceae	TRE	ACT	12441	WHI
Psychotria carthagenensis Jacq.	Rubiaceae	SBR	ACT	12286	WHI
Psychotria leiocarpa Cham. & Schltdl.	Rubiaceae	SBR	ACT	12448	WHI
Balfourodendron riedelianum (Engl.) Engl.	Rutaceae	SUB	ACT	12815	WHI
Casearia cf. *decandra*	Salicaceae	TRE	ACT	12731	WHI
Allophyllus edulis (St. Hil.) Radlk.	Sapindaceae	TRE	ACT	12319	CRE
Paullinia meliaefolia A.L.Juss.	Sapindaceae	TRE	ACT	12392	WHI
Sapindus saponaria L.	Sapindaceae	TRE	ACT	12394	WHI
Serjania communis Cambess.	Sapindaceae	CRE	ACT	12388	WHI
Crysophyllum cf. *lucentifolium* Cronq.	Sapotaceae	TRE	ACT	12776	CRE
Smilax campestris Griseb.	Smilacaceae	CRE	ACT	12399	VIN
Cestrum corimbosum Schltdl.	Solanaceae	SBR	ACT	12748	WHI
Physalis pubescens L.	Solanaceae	TRE	ACT	12505	YEL
Solanum americanum Mill.	Solanaceae	SBR	ACT	12782	WHI
Solanum atropurpureum Schrank.	Solanaceae	SBR	ACT	12407	WHI
Solanum palinacanthum Dunal	Solanaceae	SBR	ACT	12402	WHI
Solanum sp.	Solanaceae	SBR	ACT	12411	WHI
Turnera serrata Vell.	Turneraceae	HER	ACT	12372	WHI
Boehmeria nivea (L.) Gaudich.	Urticaceae	SBR	ACT	12565	CRE
Lantana trifolia L.	Verbenaceae	SUB	ZIG	12751	PIN
Lippia alba L.	Verbenaceae	SUB	ZIG	12817	PIN/YEL
Hybanthus communis (A. St. Hil.) Taub.	Violaceae	SUB	ZIG	12753	WHI
Cissus verticillata (L.) Nicolson & Jarvin	Vitaceae	CRE	ACT	12823	YEL
Cissus sp.	Vitaceae	CRE	ACT	12499	YEL

actinomorphic flowers, beekeepers in this area now know that their apiaries are surrounded by flora rich in available resources. Only 1% of the studied species had isolated flowers, and the remaining species presented flowers arranged in several types of inflorescences, these frequently being species of the family Asteraceae. Floral traits with bright colors, like white, cream and yellow, were predominant in the species visited by *Apis mellifera*. Freitas and Sazima (2006) also detected a correlation between the flower color and the frequency of pollinator visits. In summary, this work has established a comprehensive list of plants visited by *Apis mellifera* in an insular protected area, which, together with their floral characterization, can assist beekeepers in optimizing their honey production, as well as provide information about the degree of vegetative deforestation. This last aspect is important for beekeepers in the area as it can be used to certify the organic honey, which is starting to be produced.

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BOOK NOTICES

Tom S. Cooperrider. Foreword by Hope Taft. Afterword by David E. Boufford. 2010. **Botanical Essays from Kent: Some Botanical Features of a University Town in Ohio.** (ISBN 978-1-60635-043-0, hbk.). The Kent State University Press, Kent, Ohio 44242, U.S.A. (**Orders:** www.kentstateuniversitypress.com). $16.95, 89 pp., color photos, 6" × 9".

From the Publisher: During the latter half of the twentieth century, the world witnessed the rise of modern environmental movement. Chronicling this significant occurrence in Kent, Ohio, a Midwestern university town, this collection of writings and photographs captures the spirit and excitement of botanical fieldwork during the 1960s, '70s, and '80s. The Kent Bog, dedicated as a state nature preserve in 1987, is the books' focal point.

David M. Brandenburg. Foreword by Craig Tufts. 2010. **National Wildlife Federation Field Guide to Wildflowers of North America.** (ISBN 978-1-4027-4154-8, pbk.). Sterling Publishing Co., Inc., 387 Park Ave. S, New York, NY 10016. (**Orders:** www.sterlingpublishing.com). $19.95, 673 pp., 4,000 + color photos, 4¾" × 7¾".

From the Publisher: More than 2,200 species of wildflowers in a single, portable volume | More than 4,000 stunning color photographs by leading nature photographers, including details of flowers, leaves, and fruits | Wildflowers arranged by genus, with description and range map included for each genus | Captions highlighting important field marks | Information on season and habitat for each species | Fruit illustrations included for several families | Range maps showing U.S. distribution | Separate section on species introduced into North America | Quick-identification key arranged by color and shape | Detailed, illustrated visual glossary of flower parts and leaf types | Essays on wildflower habitats and conservation | Waterproof cover.

Robert P. Adams. 2011. **Junipers of the World: The Genus *Juniperus*, 3rd edition.** (ISBN 978-1-4269-5382-8, pbk.). Trafford Publishing Co., 1663 Liberty Drive, Bloomington, Indiana 47403, U.S.A. (**Orders:** www.trafford.com; orders@trafford.com; www.amazon.com; CustomerSupport@trafford.com; 1-888-232-4444; 812-355-4082 fax). $29.95, 426 pp., b/w photos, 8¼" × 11".

From the Publisher: The Junipers of the World contains a synthesis of data on evolution by examining: Geographic Variation, Speciation in Sections of the Genus, Keys to *Juniperus*, Species Descriptions, Distribution Maps, Plant Photos, Hybridization, Ecology, Cultivated Junipers, Commercial uses, Cross Indexed Synonymy of *Juniperus*, and Tables on the Leaf Essential Oils.

"An essential reference book that will be useful for herbaria, museums, wildlife biologists, range scientists, foresters, ecologists, and all who are involved in identification and study of *Juniperus* species."

K.C. Roshy. 2010. **Bamboos at TBGRI [Tropical Botanic Garden and Research Institute].** (ISBN 978-81-920098-0-3, pbk.). Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram 695562, Kerala, INDIA. (**Orders:** http://www.tbgri.in/; http://www.tbgri.in/tbgri/Bambo/bamboo.htm). $30.00, 104 pp., color throughout, 7¾" × 10¾".

Dr. K.C. Koshy has worked steadily for 24 years in building the living collection of bamboos at the Tropical Botanic Garden and Research Institute in Kerala, India. This book summarizes his stead-fast work and efforts to understand the diversity of Indian bamboos and to conserve them. Conservation of plants is aided by understanding everything possible about the plants and Dr. Koshy gives us a detailed accounting of the living collection of bamboos at TBGRI through carefully documented research. The book is divided into three chapters: **1)** Establishing a Living Collection of Bamboos. **2)** Bamboo Resources at TBGRI. In Chapter 2, the living genera at TBGRI are alphabetically arranged, followed by an alphabetical listing of the species. Each species treated includes their accepted name, synonyms and reference to major works. A brief description is followed by an overview of the living collections. Information associated with the living collections includes accession number or clump number, location, coordinates, planting date, propagule, locality, collection date, and collector and collection number. All herbarium specimens are deposited in the herbarium at TBGRI. Each species is nicely illustrated with a color photograph. **Chapter 3** is Sustainable Utilization and Future Options. Rounding out the book are References, Acronyms of Organizations, Definitions, and an Index to Bamboo Scientific Names.—*Barney Lipscomb, Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107-3400, U.S.A.*

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NEPTUNIA OLERACEA (FABACEAE) NEW TO THE CONTINENTAL UNITED STATES, WITH NEW AND NOTEWORTHY RECORDS OF SEVERAL ANGIOSPERMS IN ARKANSAS

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ABSTRACT

Neptunia oleracea is here reported as new to the continental United States. Eight additional species of angiosperms, both native and non-native to the United States, are reported as new or noteworthy for Arkansas. Six species, *Castanea mollissima*, *Euphorbia esula*, *Lemna trisulca*, *Macleaya cordata*, *Pistacia chinensis*, and *Rhus typhina*, are reported as new to Arkansas; two of which, *L. trisulca* and *R. typhina*, are native to the eastern and northern United States. The remaining four species were introduced into the United States from Europe and Asia. Additionally, the presence of *C. mollissima* and *M. cordata* in Arkansas represent the first occurrence of these species west of the Mississippi River. *Lotus corniculatus* is reported for its first occurrence in central Arkansas, and this record provides a significant expansion of its previously documented range in the state. *Celosia argentea* is reported for only its third occurrence in Arkansas.

RESUMEN

Se cita *Neptunia oleracea* como nueva para los Estados Unidos continentales. Se citan como nuevas o notables para Arkansas ocho especies aditionales de angiospermas, tanto nativas como non-nativas de los Estados Unidos. Seis especies, *Castanea mollissima*, *Euphorbia esula*, *Lemna trisulca*, *Macleaya cordata*, *Pistacia chinensis*, y *Rhus typhina*, se citan como nuevas para Arkansas; dos de las cuales, *L. trisulca* y *R. typhina*, son nativas del este y norte de los Estados Unidos. Las restantes cuatro especies se introdujeron en los Estados Unidos desde Europa y Asia. Adicionalmente, la presencia de *C. mollissima* y *M. cordata* en Arkansas representan la primera existencia de estas especies al oeste del río Mississippi. *Lotus corniculatus* se cita por primera vez en Arkansas central, y esta cita aporta una expansión significativa de su rango previamente documentado en el estado. *Celosia argentea* se cita solo por tercera vez en Arkansas.

INTRODUCTION

Numerous introductions of non-native species and range expansions of both native and non-native species have occurred in Arkansas over the past 10 years, with our (and others) field work on ruderals and recent escapes in urban environments leading to the recognition of many plant species being documented as new to Arkansas or exhibiting significant range expansion (Nesom 2009; Peck 2003; Peck & Serviss 2006; Serviss 2006; Serviss et al. 2006, 2007a, 2007b; Serviss & Peck 2008; Serviss 2009). Many of these species when initially encountered were present as a single, spontaneous individual or as a relatively small, isolated population; however, subsequent to discovery, some have increased in numbers (Serviss 2006). Spontaneous is used here to mean the autonomous occurrence through sexual or asexual reproduction of a plant species in a region or flora to which it is not native. It is equivalent to the term "escaped" as defined by Nesom (2000).

Non-native plant species have frequently not been adequately documented and incorporated into North American floristic studies (Neves et al. 2009). It is therefore highly imperative that continued documentation and subsequent investigation be focused on the occurrence and biology of non-native species both in the state's flora and nationally. Many of these species are initially represented in our flora as waifs from repeat accidental introductions (this is typical from ballast or rubbish discards), or as local escapes from cultivated ornamentals. Subsequent to introduction, they demonstrate an ability to persist or establish, with some eventually becoming invasive. Therefore, a heightened level of awareness, documentation, and attention must be afforded to non-native species in floras and herbaria, as supported by Pyšek et al. (2004). Instead of being dismissed and ignored when initially encountered, which over time may lead to the probability of

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control or eradication being minimized or lost, a heightened level of awareness, documentation, and attention must be afforded to non-native species in our flora.

The occurrence and distribution data of the taxa listed below was determined from the on-line national flora database, PLANTS Database (USDA, NRCS 2008).

NEW SPECIES RECORD FOR THE CONTINENTAL UNITED STATES

Neptunia oleracea Lour. [syn. *N. prostrata* (Lam.). Baill.] (Fabaceae). Garden puff or water mimosa (Figs. 1, 2) is an aggressive and invasive aquatic species, presumably native to India and southeastern Asia (possibly also tropical Africa), where it is used as an edible food plant; however, its present distribution is pantropical (Windler 1966). It has previously been reported from Puerto Rico, but no previous records exist for its spontaneous occurrence in the United States (Isely 1998; USDA, NRCS 2008). It is reported here for the first time in the continental United States, along the flood plain of the Little Maumelle River in Pulaski County, Arkansas. At this site, it co-occurred with *Hydrilla verticillata*. *Neptunia oleracea* is sometimes sold in the water-garden trade across the southeastern United States in USDA hardiness zones 9–11. It is called water sensitive plant or garden mimosa in the trade. Once established, it spreads rapidly across the surface of the water, aided or buoyed by white, spongy aerenchyma tissue underneath trailing stems. *Neptunia oleracea* is extremely similar morphologically to *N. plena* (water dead and awake), but can be distinguished from it and the two other species of *Neptunia* that occur in the continental United States by the following key (adapted from Windler 1966):

KEY TO SPECIES OF *NEPTUNIA* IN THE CONTINENTAL UNITED STATES

1. Plants of wet habitats (*N. plena* can also occur in moist terrestrial sites), typically growing at edge of water or directly within; floating and submergent stems often inflated with white to yellowish-brown aerenchyma tissue and rooting vigorously at the nodes; rare, currently only known from southeastern Texas (*N. plena*) or Arkansas (*N. oleracea*).
   2. Stems typically erect and often highly branched; leaves with a conspicuous gland at the base to slightly below the lowermost (proximal) pair of pinnae, pinnae (2–)4–5 per leaf, sometimes more, typically 20 or more pairs of leaflets per pinna ____ **N. plena**
   2. Stems typically prostrate with little to no branching; leaves without a gland between to slightly below the lowermost pair of pinnae, pinnae 2–4 pairs per leaf, often less than 4, 20 or fewer pairs of leaflets per pinna ____ **N. oleracea**
1. Plants completely terrestrial, possibly of moist sites but not aquatic, stems not inflated; widespread in the US.
   3. Leaflets 18–30 per pinna; inflorescence bearing 30–60 flowers, all flowers bearing stamens with functional anthers ____ **N. lutea**
   3. Leaflets (24–)30–50 per pinna; inflorescence with less than 30 flowers, the lower flowers with the stamens modified into staminodes ____ **N. pubescens**

Voucher specimen: **Pulaski Co.:** large colony clambering over surface of water, Little Rock, Little Maumelle River, near Two Rivers Park, along Arkansas River flood plain, 18 Sep 2009, *Peck 09-555* (HEND).

SPECIES NEW OR NOTEWORTHY FOR ARKANSAS

Castanea mollissima Blume. (Fagaceae). Chinese chestnut is a large, deciduous tree to 18 m or more tall that is native to China and Korea. This is the first documentation of this species in Arkansas, and may be the first record of it outside of cultivation west of the Mississippi River. *Castanea mollissima* is also known from several eastern states, ranging from Illinois and Alabama eastward to Massachusetts and Florida. *Castanea mollissima* can be confused with *Castanea pumila* (chinkapin) in Arkansas, but can be distinguished by the following key:

KEY TO SPECIES OF *CASTANEA* IN ARKANSAS

1. Infructescence generally consisting of several involucres, bracts narrow, 2.5–3.8 cm in diameter with only a single nut present ____ **C. pumila**
1. Infructescence consisting of only a single involucrate set of bracts, bracts wider, 3–6 cm in diameter, usually with 2–3 nuts ____ **C. mollissima**

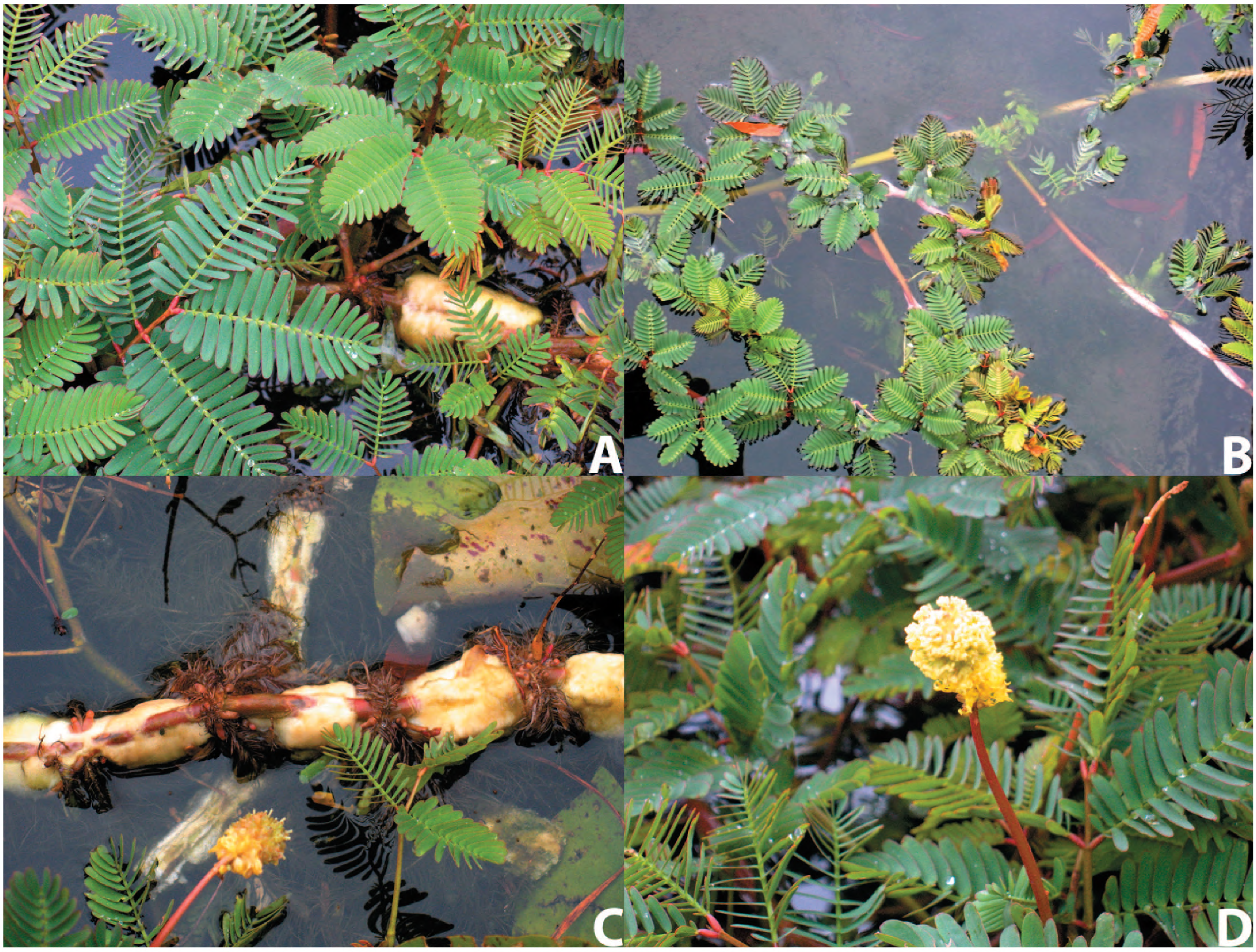

Fig. 1. Plant and habit for *Neptunia oleracea* (photographs are of plants naturalized in Pulaski County, Arkansas). A. Leaves. B–C. Stems, without and with aerenchyma tissue. D. Flowers.

Voucher specimen: **Clark Co.:** four spontaneous plants in disturbed open lot and adjacent woods, McNeely Road, S of the intersection of Eckels Road and McNeely Road, Central Community, 24 Oct 2010, *Serviss 7410* (HEND).

Celosia argentea L. [syn. *C. cristata* L.] (Amaranthaceae). Silver cock's comb or crested cock's comb is a commonly cultivated, ornamental, annual species native to India. It is naturalized in at least 22 eastern states, including Arkansas; however, this record represents only the third collection of it in the state outside of cultivation, as it was previously known only from Baxter and Cross counties (Sarah Nunn, pers. comm.)—reported as *C. cristata*, AVFC (2006). *Celosia argentea* is probably more common in the state's flora than collections indicate, as it is frequently cultivated and readily sets seed, often culminating in the production of numerous additional plants.

Voucher specimen: **Clark Co.:** large population with dozens of individuals and no cultivated plants present in the vicinity, plants did not closely resemble cultivated forms, 80+ cm tall, silver-colored calyces tinged with bright pinkish-red coloration, growing along edge of and in seasonally wet area adjacent to the Ouachita River, Ouachita Baptist University, Arkadelphia, 8 Sep 2009, *Serviss 7407* (HEND).

Euphorbia esula L. (Euphorbiaceae). Leafy spurge or wolf's milk is a highly invasive perennial native to Europe. This is the first record of this species from Arkansas, though outside of the southeastern United States and the southern plains, it is well established (and invasive). *Euphorbia esula* can easily be confused with another, introduced species of spurge naturalized in Arkansas, *E. cyparissias* (cypress spurge). The two species can be distinguished using the following key:

Fig. 2. Herbarium specimens of *Neptunia oleracea* (specimens from Pulaski County, Arkansas). A–B. Floating stems showing aerenchyma tissue, leaves, and adventitious roots. C. Stem without aerenchyma tissue.

KEY TO DISTINGUISH *EUPHORBIA ESULA* FROM *E. CYPARISSIAS* IN ARKANSAS

1. Principle cauline leaves linear to linear-filiform or spatulate, 0.5–3 mm wide, spaced 2–20 per centimeter of stem; floral leaves (those subtending the cyathia) 4–6 mm long, much less than 1 cm long ______ **E. cyparissias**
1. Principle cauline leaves lanceolate to oblong-lanceolate, sometimes narrowly so, (2–)3–10 mm wide, spaced 0–5 per centimeter of stem; floral leaves 10–13 mm long ______ **E. esula**

Voucher specimen: **Pulaski Co.:** several dozen plants in two colonies along edge of bike trail in open woods with loose sandy soil, Little Rock, Two Rivers Park, 21 Jul 2010, *Peck 2010279* (HEND).

Lemna trisulca L. (Araceae). Star duckweed is native to Canada and most of the continental United States, with the exception of a few southeastern states. This is the first confirmed record of this species from Arkansas. Previously, *L. trisulca* was placed on the Arkansas flora checklist (AVFC 2006) based on a literature reference by Landolt (1986) who reported an occurrence in Fulton County, but did not cite a voucher specimen.

Voucher specimen: **Pulaski Co.:** several colonies 0.5–1 m across at edge of Little Maumelle River at Two Rivers Park boat launch, 21 Jul 2010, *Peck 2010277* (HEND).

Lotus corniculatus L. (Fabaceae). Bird's-foot trefoil is a perennial herb native to Europe, but naturalized over much of the United States. *Lotus corniculatus* is uncommon in Arkansas and this is the first record of it outside of northern Arkansas. It has previously been recorded from Benton, Carroll, Fulton, and Washington counties (Brent Baker, pers. comm.).

Voucher specimen: **Pulaski Co.:** several plants on bank near boat launch on Little Maumelle River, Two Rivers Park, Little Rock, 21 Jul 2010, *Peck 2010281* (HEND).

Macleaya cordata (Willd.) R. Br. (Papaveraceae). Plume-poppy or tree celandine is native to China and Japan, but is sporadically naturalized in Canada and the eastern United States. Our record from Arkansas represents the first published occurrence of *M. cordata* west of the Mississippi River. Although this is the first

published record of *M. cordata* from Arkansas, the species was actually previously collected in Washington County along a roadside south of Rogers by Aileen McWilliam on 9 July 1960. The McWilliam specimen was sent unidentified from UARK to NCU as part of a massive thinning of old and duplicate specimens, without retention of a duplicate specimen. The specimen at NCU [NCU 212600] was determined as *M. cordata* by R. W. Kiger in 1983. The species was not listed for Arkansas by Smith (1988), nor more recently by Kiger (1997) or the Arkansas Vascular Flora Committee (2006), but was attributed to the state in the PLANTS Database (USDA, NRCS 2008).

Voucher specimen: **Pulaski Co.:** one, multi-stemmed plant, ca. 3 m tall, in an open, sandy field, Little Rock, Two Rivers Park, 20 Aug 2010, *Peck 10-0775* (HEND).

Pistacia chinensis Bunge. (Anacardiaceae). Chinese pistachio is a large, deciduous tree to 18 m tall that is native to China. This is the first documentation of this species in Arkansas outside of cultivation. It has been previously documented from Alabama, California, Georgia, Oklahoma (Serviss 2006), and Texas. This species was planted in many locations in Little Rock over the past 20 years, and a few adventive plants have been found peripheral to a staging nursery. Additional spontaneous plants should be expected elsewhere in Arkansas. Vegetatively, *P. chinensis* somewhat resembles a few other woody species present in the Arkansas flora, including *Ailanthus altissima* (tree-of-heaven), *Sapindus drummondii* (western soapberry), and the three arborescent species of *Rhus* (sumac), but can be distinguished from them by the following key:

KEY TO *PISTACIA CHINENSIS* AND SIMILAR WOODY SPECIES IN ARKANSAS

1. Leaflets entire except for a few large teeth at the base, each tooth on its undersurface with a large, plate-shaped gland at the apex; fruit a samara ____ **Ailanthus altissima**
1. Leaflets entire or toothed, but if toothed, teeth lacking a large, plate-shaped gland at the apex; fruit a drupe.
   2. Rachis of leaf prominently winged ____ **Rhus copallina**
   2. Rachis of leaf without wings or wings very narrow and obscure (sometimes present in *Sapindus*).
      3. Leaflets entire (*Sapindus* occasionally with a few toothed leaflets).
         4. Foliage strongly (anacardiaceous) aromatic, upper surfaces of leaflets semi-glossy; twigs with a large, brown or sometimes red, conical-shaped terminal bud; flowers red to reddish-green; drupes red at maturity, eventually turning dark blue, not translucent ____ **Pistacia chinensis**
         4. Foliage without strong, aromatic odor, upper surfaces of leaflets dull; twigs without a terminal bud; flowers yellowish-white; drupes golden-yellow and translucent at maturity ____ **Sapindus drummondii**
      3. Leaflets prominently toothed.
         5. Rachis and lower surfaces of leaflets glabrous or nearly so ____ **Rhus glabra**
         5. Rachis and lower surfaces of leaflets densely velutinous-pubescent ____ **Rhus typhina**

Voucher specimen: **Pulaski Co.:** six spontaneous plants under the Arch Street Bridge, Little Rock, 3324 S Arch Street behind City of Little Rock Landscape Shop, 8 Oct 2009, *Duckett 76* (HEND).

Rhus typhina Torner (Anacardiaceae). Staghorn sumac is a deciduous shrub or small tree to 10 m tall that is native to the eastern United States and southern Canada. This is the first documentation of this species outside of cultivation in Arkansas. *Rhus typhina* resembles the other two arborescent species of sumac that occur in Arkansas, *R. glabra* (smooth sumac) and *R. copallina* (winged sumac), but can easily be distinguished using the key above.

Voucher specimen: **Pulaski Co.:** one spontaneous plant, spreading vegetatively by root suckers, at boat launch on the Little Maumelle River, Little Rock, Two Rivers Park, 21 Jul 2010, *Peck 2010283* (HEND).

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We would like to very sincerely thank Ann Willyard (Hendrix College), Kristen Benjamin (Henderson State University), and one anonymous reviewer for their extremely helpful comments and suggestions regarding this paper. We would also like to thank Brent Baker (Arkansas Natural Heritage Commission) and Sarah Nunn (University of Arkansas, Fayetteville) for providing species distribution data for Arkansas. Additionally, we would like to thank Betty Patton for her assistance in acquisition of some voucher specimens.

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FIRST RECORD OF *IRIS PSEUDACORIS* (IRIDACEAE) FROM COLORADO

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ABSTRACT

Iris pseudacorus L. (Iridaceae) is reported for the first time for Colorado.

Key Words: *Iris pseudacorus*, Colorado, non-native

RESUMEN

Iris pseudacorus L. (Iridaceae) se cita por primera vez para Colorado.

INTRODUCTION

Iris pseudacorus L. (Iridaceae) is a non-native obligate wetland perennial that is widely established across the United States and Canada (Henderson 2002; USDA, NRCS 2011). It is native to Eurasia and northern Africa (Sutherland 1990). The earliest records of this plant in North America appear to be from the north-eastern United States and Canada. Cody (1961) cites a Fernald & Wiegand collection from 1911 as being the first record from Canada. The plant was listed as a rare escape from gardens in Connecticut by Graves et al. (1910). This *Iris* species is widely cultivated and has been in use in North American gardens since as early as the 18th century (L.H. Bailey Hortorium 1976; Wells & Brown 2000). *Iris pseudacorus* is listed on the Noxious Weed list in 5 states, with some states listing it as banned (i.e., importation, sale, and trade are prohibited) (USDA, NRCS 2011). However, there have been few studies conducted to quantify its threats (but see Thomas 1980).

NEW RECORDS FOR COLORADO

Iris pseudacorus has not been previously reported for Colorado in floristic treatments covering the state (Harrington 1964; Weber & Wittmann 2000; Hartman & Nelson 2001; Snow 2009) or Boulder County specifically (Hogan 1993; Weber 1995). In addition, no Colorado specimens were located in a search of COLO and KHD or through an online database search of CS and RM (Southwest Environmental Information Network 2011).

Voucher Specimens: **COLORADO. Boulder Co:** S of Lyons near, in irrigation ditch between open field and houses, 40.215722 N -105.266522 W, elev. 1626 m, locally common, 28 Jun 2010, *M.W. Denslow & M.L. Denslow 2675* (BOON, duplicates to be distributed); Park S of Lyons, along banks of St. Vrain River, 40.219675 N -105.265481 W, elev. 1627 m, uncommon at rivers edge, 29 Jun 2010, *M.W. Denslow 2676* (BOON, duplicates to be distributed); SE of Boulder along Bobolink Trail on E side of Boulder Creek, wet depression, 39.999015 N -105.215029 W, elev. 1614 m, locally abundant, 2 Jul 2010, *M.W. Denslow, G.L. Katz & M.L. Denslow 2677* (BOON, duplicates to be distributed).

DISCUSSION

The three specimens cited represent two distinct populations, each with several individuals of this species. This species is an established part of the Colorado flora. Extensive surveys for this plant have not been conducted, so its range in Colorado is not clear at this time. However, additional populations have been observed along Boulder Creek. It is also unclear how long this species has been established in the wild, since the vouchered populations do not appear to be newly established. This species has been cultivated on the campus of The University of Colorado, Boulder since at least the 1970s.

The only other documented species of *Iris* present in Colorado is the native *I. missouriensis* Nutt. (Hartman & Nelson 2001). *Iris missouriensis* is unlikely to be confused with *I. pseudacorus* because the former has a blue to lavender perianth as opposed to a yellow perianth in the latter. We have also observed *I. germanica* L. persisting in areas where gardeners have discarded rhizomes. This widely cultivated species can have a broad range of perianth pigmentation from blue-violet to white, including yellow. However, *I. germanica* differs most notably from both *I. missouriensis* and *I. pseudacorus* by the presence of multicellular hairs on the sepals (Henderson 2002).

These records of *I. pseudacorus* are significant for two reasons. First, this is the first report of this species from the state of Colorado outside of cultivation. Further, there are currently no records from the neighboring states of Wyoming, New Mexico or Arizona (USDA, NRCS 2011). Second, this species is a listed Noxious Weed and is regulated in some states (USDA, NRCS 2011). Therefore this species may require management action in Colorado. Sources of information on the control of *I. pseudacorus* mention mechanical removal and chemical application as the main methods of control (e.g., Stone 2009). However, it should be noted that these methods may be problematic in the habitats typical of this species. Research is needed to assess the effects of control measures on wetland and aquatic communities. The best way to stop *I. pseudacorus* from entering new watersheds may be to limit its use in horticulture (Reichard & White 2001).

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BOOK NOTICE

Douglas J. Futuyma, H. Bradley Shaffer, and Daniel Simberloff, eds. 2010. **Annual Review of Ecology, Evolution, and Systematics, Volume 41.** (ISSN 1543-592X; ISBN 978-0-8243-1441-5, hbk.). Annual Reviews, Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.AnnualReviews.org, science@annualreviews.org, 800-523-8635, 650-493-4400). $84.00 indiv., 419 pp., 7⅝" × 9⅜".

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NATURALIZED YELLOW COWHORN ORCHID, *CYRTOPODIUM FLAVUM* (ORCHIDACEAE), SPREADING IN FLORIDA

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ABSTRACT

The yellow cowhorn orchid, *Cyrtopodium flavum*, has been naturalized in a small area of Miami-Dade County in southeastern Florida since the early 1970s. We recently observed an alien oil-collecting bee *Centris nitida* pollinating *C. flavum* in Florida, an activity that could promote the spread of the weed. We investigated the spread of the orchid and found it at twelve sites and in two additional counties; Broward County to the north and Collier County to the west. The natural area most suited for the orchid are the pine rocklands of Miami-Dade County, a native vegetation type that has been greatly diminished by development. Evidence of flower visitation (pollinia removal or fruit set) was found in the counties where *C. nitida* is widely established. Although the orchid appears to be spreading, it is a rarely encountered plant that is unlikely to become an aggressive weed in Florida.

RESUMEN

La orquídea amarilla cuerno de vaca, *Cyrtopodium flavum*, se ha naturalizado en una pequeña área del Condado de Miami-Dade en el sureste de de Florida desde los inicios de los 70. En un reciente estudio nosotros encontramos que un abeja introducida colectora de aceite, *Centris nitida*, poliniza esta planta y por tanto puede promover su dispersión como una maleza. En este estudio investigamos la distribución de esta orquídea y encontramos que en la actualidad se encuentra en doce localidades y en dos condados adicionales; Condado de Broward en el norte y Condado de Collier en el oeste. El área natural más adecuada para esta especie es el pinar sobre roca del Condado de Miami-Dade, una comunidad de área reducida y alto valor. Aunque al parecer esta orquídea ha ido aumentando su área de de dispersión, aún tiene una modesta presencia en Florida.

The yellow cowhorn orchid, *Cyrtopodium flavum* Link & Otto ex Rchb. is a terrestrial orchid native to the eastern coast of Brazil (Romero-Gonzalez et al. 2008). It was first found to be naturalized in Florida during the early 1970s (Hammer 2001). The earliest specimen that we are aware of was collected by George Avery (*Avery 1155* in the herbarium of the Fairchild Tropical Botanic Garden, FTG) on May 12, 1972, from plants that volunteered on gravel inside a screened porch in Miami-Dade County (Hammer 2001). Hammer (2001) and McCartney (2010) discuss Avery's notes on the cultivation of the orchid during the 1950s and the early naturalization. Luer (1972) included the orchid in his book "The native orchids of Florida" as *C. andersonii* (Lamb. ex Andrews) R. Br. from South America and said it occurred in the Everglades. The orchid was also known as *C. polyphyllum* (Vell.) Pabst. ex F. Barrios, until Romero-Gonzalez et al. (2008) decided that it was conspecific with *C. flavum*.

For many years the orchid appeared to be limited to Kendall, a suburb of Miami in the southwestern urban area of Miami-Dade County. The primary location of the orchid is a pine rockland preserve known as "Boystown" at 25 39 28N by 80 25 16W, where we estimated there to be 10,000 mature plants (Liu & Pemberton 2010). The yellow cowhorn orchid also appeared periodically in residential gardens in Kendall.

We studied the pollination of the orchid (Liu & Pemberton 2010) and found that it is being pollinated by an alien bee, *Centris nitida* Smith, a bee native to Central and South America that we had found to be naturalized in Florida (Pemberton & Liu 2008a). Only about 1% of the flowers set fruit, but given the large

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number of seed per fruit (ca. 100,000 and 320,000 in two examined fruit) and large number of reproductive plants at the site, the total number of seed produced is very large. The advent of this alien pollinator and the resulting large number of seed being produced as the site could foster the spread of this alien orchid in southern Florida. The goal of this study was to attempt to learn if *C. flavum* has spread beyond the Kendall area, and if so what the current distribution of the orchid is. Orchids rarely naturalize because of the lack of specialized pollinators and mycorrhizae, and are highly underrepresented in invasive taxa (Daehler 1998; Pemberton & Liu 2009). The yellow cowhorn orchid is of interest because it is one of the rare orchids that has overcome these barriers to naturalization.

METHODS

We discussed our interest to locate new occurrences of *C. flavum* with field biologist colleagues at public and private organizations, as well as land managers at county, state and federal levels in southern Florida, and requested locality data, photographs, and specimens on suspected occurrences. We checked various data bases such as the Florida Atlas of Vascular Plants and the extensive natural areas plant inventory data base of the Institute of Regional Conservation, as well the primary herbaria in the state for records of the orchid. Flowering specimens of the orchid were taken to the meetings of the Dade Chapter of the Florida Native Plant Society and the Fort Lauderdale Orchid Society with a request for members to report occurrences of the orchid that they encounter to us.

RESULTS

We found ten new occurrences of *C. flavum*, with all but one coming from field biologist-land manager colleagues. The current known distribution is shown in the map (Fig. 1), which includes the new locations and previously known locations at Boystown and a Kendall residence. The map includes natural areas where *C. flavum* plants were found and subsequently removed due to the orchid being a non-native invader. We found that the orchid has spread to Broward County in the north to a site 80 km from the Boystown site, to the northern part of Everglades National Park 104 km to the west of Boystown, to Collier County to the Fakahatchee State Botanical 103 km to the west, and to Seminole Collier County State Park, 122 km to the west. Within Miami-Dade County notable occurrences were found in the pine rockland preserves at the Miami Zoo and at the adjacent Coast Guard property.

Descriptions of the occurrences

Collier County.—The Fakahatchee Strand plants (reported by Mike Owen) were found in two patches along the shoulder of the Jane Road, which is elevated above the lower wetland habitat through which it runs. During the June, 2008 visit, three plants were found at the first site, none of which were in flower or bore old inflorescences. At the second site, a few hundred meters away, a single plant was found and it was in flower. Pollinia removal was scored and no pollinia had been removed in the 18 open flowers. No fruit were found.

The Collier Seminole State Park occurrence (reported by Patel Maulik and Dennis Giardina) involved a single plant growing at the base of a pine tree in a raised dry situation in undisturbed native vegetation. The plant, which was first noted in 2007, flowered in 2009.

Miami-Dade County.—The Everglades National Park (in the western part of Miami-Dade County), occurrence (reported by Jimi Saddle) was of plants growing on an abandoned asphalt road near the entrance of Shark Valley. The road is elevated above the wetter surrounding land. When the site was examined in June, 2008, six plants were found, including five that had flowered in that year or the previous year. Two of these plants bore a single fruit each. The plants were removed.

Two plants, one in flower, were found at Bill Baggs Cape Florida State Recreation Area on Key Biscayne by Liz Golden during the 1990s (reported by Keith Bradley).

Plants at the Dolphin Center Addition adjacent to the Dolphin Stadium parking lot in northern Miami-Dade County were found by Keith Bradley in May, 2006. During our visit in March, 2009, we found 10

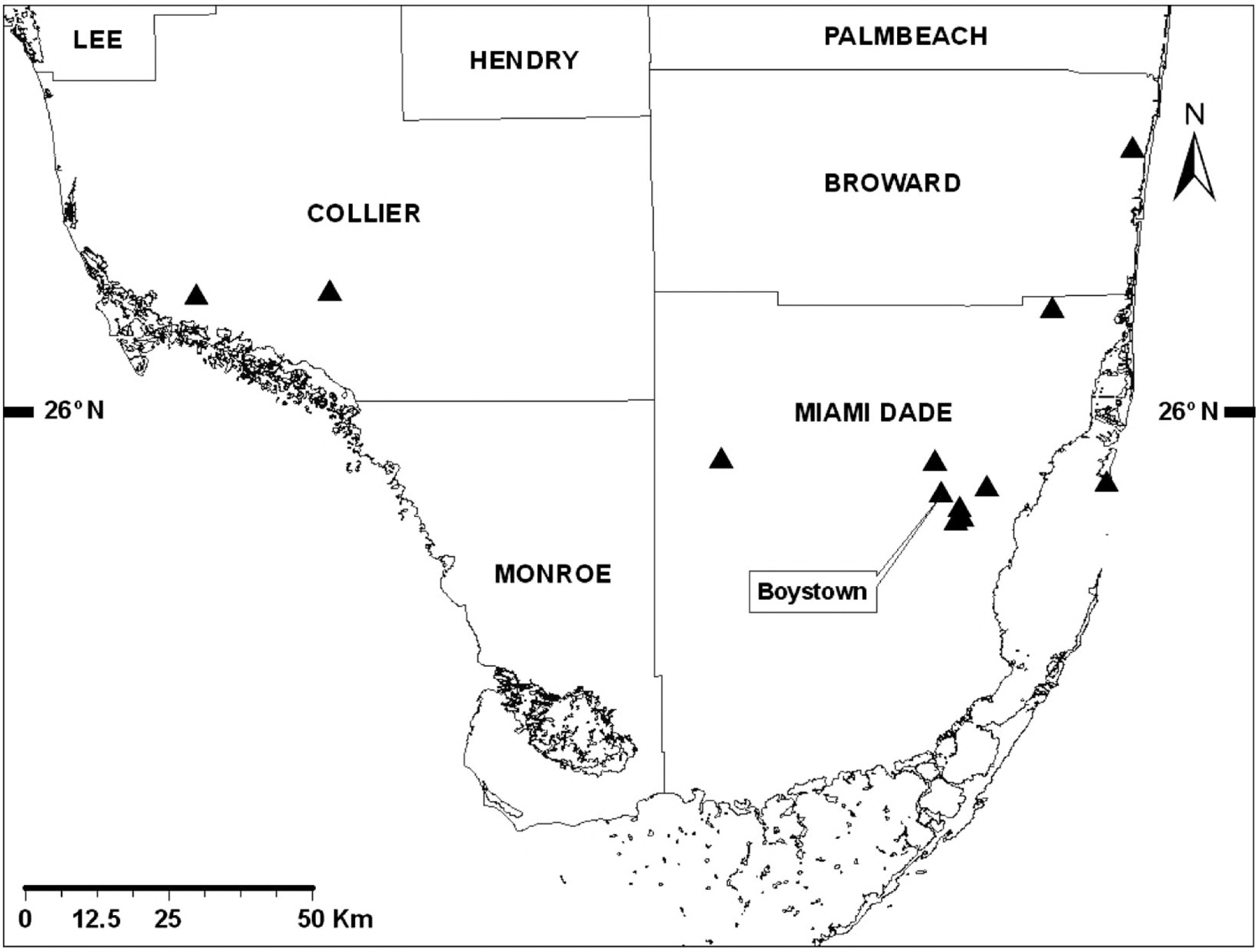

Fig. 1. Map of the known distribution of the invasive orchid, *Cyrtopodidum flavum*, in Florida.

plants within a 6m^2 space on the slope of an artificial berm above the stadium parking lot. Only two of the plants were of reproductive size and one bore an old flower stalk, but no fruits were found. We were unable to see flowers because *Cyrtopodium flavum* blooms in southern Florida during May and June.

A single flowering plant was found at Ron Ehmann Park in the City of Miami in March, 2010, by Sonya Thompson and sprayed with herbicide.

The largest intact population of *C. flavum* discovered was at the pine rockland preserve at the Miami Zoo reported by Jennifer Possley. We visited the site on March 10, 2008, two months prior to the flowering season. Mature and immature plants were scattered in an area ca. 100m by 50m. Twenty five plants were assessed for past reproductive status and four were found to have old flower spikes, and one of these bore a fruit from the previous season. This pineland is undisturbed and composed of native vegetation with well spaced *Pinus ellioitii* Engelm. and saw palmetto palms (*Serenoa repens* (W. Bartram) Small). The only apparent exotic plant was another invasive orchid, *Eulophia graminea* Lindl., which has recently found to be naturalized in Miami-Dade County (Pemberton et al. 2008). The pine rocklands are a diminishing habitat containing many rare species threatened by development (Synder et al. 1990).

Two plants were found at the pine rockland site at the Coast Guard property in Miami near the Miami zoo by Tony Pernas in 2007. Both had previously flowered and both were removed.

In March 2010, between 25 and 50 *C. flavum* plants were removed from the Gold Coast Railroad Museum pineland by Sonya Thompson and Pete Diamond. This pineland is contiguous with the Coast Guard property and the Miami Zoo pinelands. Some of the plants bore old flower stalks.

Broward County.—The Broward County record is in a residential area along the border of two residences (reported by Bruce and Susan Munz via Dot Henley). The site was visited on May 31, 2008. The plants consist of a large flowering patch ca. 2 m by 1 m. Pollinia removal was scored and found to be 3/100 sampled flowers. No fruit were present. The occupants of both houses thought that the residents in the other house had planted the orchid, but both denied that they did. Mr. Munz estimated that the plant had been there at least three years. This was the only new occurrence in a residential area and the only report resulting from an orchid club member.

Other.—Finally, there are a few plants of *C. flavum* growing in a flower bed outside the Environmental Horticulture building of the University of Florida in Gainesville, in northern Florida (Daniella Dutra reporting). When the plants were investigated during the spring of 2009, they were regrowing after being severely damaged by freezing temperatures during the winter, but the freezes of 2010 appears to have killed the plants (Mark Whitten, pers. comm.). The origin of these plants is unknown, but we felt that the occurrence outside of a horticultural research center strongly suggests transplantation rather than natural spread.

DISCUSSION

Although the geographic area where the yellow cowhorn orchid now occurs appears to be large, the amount of suitable natural habitat in this area is small. Most of the land within the orchid's Florida distribution floods seasonally so is unlikely habitat for *C. flavum*. In the plant's native Brazil, it commonly grows on rock and sand (Pansarin et al. 2008a, b). The pine rockland habitat that the orchid grows on in Miami-Dade County are the most elevated natural habitats in southern Florida and are probably the most suitable habitat in southern Florida. The large population at the Boystown site is also a pine rockland. The road surface in Everglades National Park and elevated roadsides in the Fakahatchee Strand where *C. flavum* are found are probably the only suitable habitat available in the otherwise wet habitats. Likewise the Dolphin Stadium berm and the residential area in Broward are also artificially elevated.

Pine rocklands, which are limited to Miami-Dade County, appear to be most subject to invasion by *C. flavum*. Once established in this habitat, the orchid can be difficult to control. At Boystown, managers used repeated herbicide treatments to attempt to control the orchid but failed (Cristina Rodriguez, pers. comm.). The yellow cowhorn orchids at the site also survived fires and may have been promoted by fire. Because of the ecological value of this limited habitat, we recommend that *C. flavum* plants invading pine rocklands should be removed.

Fruit production or evidence of pollinator visitation, through pollinia removal from flowers, was observed in plants in Broward and Miami-Dade counties but not in plants in Collier County. The known pollinator of this orchid, *Centris nitida*, also occurs widely in Broward and Miami-Dade counties. *Centris nitida*, however, may not occur in the Shark Valley area of Everglades National Park in the far western part of the county, where fruit set was observed. The native oil-collecting bee, *C. errans* Fox, which pollinates congeneric Florida native cowhorn orchid, *Cyrtopodium punctatum* (Pemberton & Liu 2008b) might be responsible.

Both R. Hammer (Hammer 2001) and the lead author observed cultivated plants in their yards to spread to areas with woodchip mulch, presumably by seed. Given how readily the orchid spread locally to mulched areas, it is surprising that the orchid was not found more frequently in the landscapes of residential, educational and commercial sites, where woodchip mulch is extremely common.

The spread and increased geographic distribution of *C. flavum* is modest, particularly in comparison to the recently naturalized orchid *Eulophia graminea*. *Cyrtopodium flavum* has been established in southern Florida for about 40 years, although how long it has had an effective pollinator is unknown. It now occurs in three counties. *Eulophia graminea* was found to be established in 2007 and was known to occur at five sites in a single county (Miami-Dade County) in 2008 (Pemberton et al. 2008). By 2010, it has spread to 67 locations in seven counties (Pemberton, submitted). One difference is that *Eulophia graminea* sets more fruit than *C. flavum* (4.5 and 9.2% vs.1%) (Pemberton et al. 2008, Liu & Pemberton 2010), but the fruits of

C. flavum are bigger and probably contain more seed. *Eulophia graminea* also appears to have the ability to grow in more diverse habitats both in its native area (Pemberton et al. 2008) and in Florida than does *C. flavum* (Pansarin et al. 2008a, b).

One possible threat that the spread of *C. flavum* creates is the hybridization with the rare native congener *C. punctatum* and the dilution of its gene pool. In an earlier study we were able to produce fruit in *C. flavum* by hand transferring pollinia of *C. puncatum* (Liu & Pemberton 2010), demonstrating, in part, the ability of the plants to hybridize. Although natural hybridization between the two species is possible, it is unlikely due to little overlap in flowering phenology (primarily March and April in *C. puncatum* and May and June in *C. flavum*), different habitats (primarly pine rocklands in *C. flava* and swamps for *C. punctatum*), and as far as is known, different species of *Centris* bee pollinators.

ACKNOWLEDGMENTS

We thank the following people for providing locality records for *C. flavum*: Keith Bradley, Pete Diamond, Dennis Giardina, Dot Henley, Patel Maulik, Bruce and Susan Munz, Mike Owen, Tony Pernas, Jennifer Possley, Jimi Saddle, Karen Relish. Joanne Pemberton developed the map and Javier Francisco Ortega provided the Spanish abstract. William Mark Whitten gave us a constructive and helpful review.

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BOOK NOTICE

Sabeeha Merchant, Winslow R. Briggs, and Donald R. Ort. 2011. **Annual Review of Plant Biology, Volume 62.** (ISSN 1543-5008; ISBN 978-0-8243-0662-5, hbk.). Annual Reviews, Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.AnnualReviews.org, science@annualreviews.org, 800-523-8635, 650-493-4400). $91.00 indiv., 611 pp., 7⅝" × 9⅜".

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J. Bot. Res. Inst. Texas 5(1): 336. 2011

NATURALIZATION OF THE NUN'S HOOD ORCHID (*PHAIUS TANKERVILLEAE:* ORCHIDACEAE) IN CENTRAL FLORIDA

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ABSTRACT

A large, old population of the non-native, ornamental nun's hood orchid, *Phaius tankervilleae*, was discovered in a native forest in central Florida. This is the first report of naturalization of this Asian terrestrial orchid in central Florida, and the second report for the state. Although relatively few orchids naturalize, in comparison to other plant groups and the large number cultivated, there are 11 naturalized orchids in Florida.

RESUMEN

Una gran población antigua de orquídeas no nativas, ornamentales de orquídea monja, *Phaius tankervilleae*, fue descubierta en un bosque nativo en el centro de Florida. Esta es la primera cita de la naturalización de esta orquídea terrestre de Asia en el centro de Florida, y la segunda en el estado. Aunque relativamente hay pocas orquídeas naturalizadas en comparación con otros grupos de plantas y el gran número de cultivo, hay 11 orquídeas naturalizadas en la Florida.

Plants of the nun's hood orchid, *Phaius tankervilleae* (Banks ex L'Hér.) Blume, were found in Weeki Wachee State Park in Hernando County (near the western coast of Florida north of Tampa) in April, 2010. This orchid population is located in a hydric hammock forest on the south side of the Weeki Wachee River. During the summer of 2010, the area was surveyed by walking zigzig transects, ca. 3 meters apart, flagging plant clumps as they were encountered. Using this method, we estimate that there are ca. 500 plants at the site. The number of pseudobulbs in the marked clumps was noted and they generally ranged from 5–19 per clump, but some had as few as 1–3, and one clump had more than 45 pseudobulbs. Points along the outer edges of the population were marked with a GPS unit in order to determine its area. This provided an estimate that the area containing the population of the *Phaius* is ca 2.3 hectares. The central location of the population is N 28 31 04.0 W 82 34 32.4. The average elevation of the site is estimated to be 10 m above sea level.

The hydric hammock where the plants were found has the soil type of Anclote Fine Sand and the most frequent canopy trees in this native forest are *Acer rubrum* L., *Juniperus virginiana* L., *Magnolia virginiana* L., *Nyssa sylvatica* var. *biflora* (Walter) Sarg., *Persea palustris* (Raf.) Sarg., *Quercus laurifolia* Michx., *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f., and *Taxodium distichum* L., Orchids growing in association with the nun's hood orchid are the following native species: *Habenaria floribunda* Lindl., an unidentified *Spiranthes* sp., *Ponthieva racemosa* (Walter) C. Mohr, and *Platanthera flava* (L.) Lindl.; and the naturalized *Oeceoclades maculata* (Lindl.) Lindl.).

Some plants were in flower in April, although freezes in December, January and February, including one on January 7, when the temperature dropped to ca. -10C, appeared to have damaged most of the plants.

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Plants were surveyed for capsules at end of July but none were found. Young plants thought to be seedlings were found at the site well away from adult plants. Considerable vegetative reproduction of the nun's hood orchid could have occurred at the site, with not only lateral expansion in the growth of clumps but also of plants generated from the fallen, fleshy flower spikes. The number of plants and pseudobulbs in the clumps, and the area occupied by the orchid suggest that the *P. tankervilleae* has been at this site for many years.

This large *Phaius* population may have originated from plants cultivated in the park when it was a tourist attraction prior to its designation as a state park 2008. One of us (DJR) worked at the park in late 1980s when the spring was tourist attraction and made some relevant observations. The director of landscaping during that period was also a commercial orchid grower who could have planted *P. tankervilleae* at the site. During that period some tender ornamentals were planted in the hammock before winter to provide them with a more sheltered environment. *Phaius tankervilleae* may have been among the plants moved into the hammock.

This extensive *Phaius* population in a natural environment is the second such occurrence in Florida. The other population is in Hardee County, northwest of Lake Ocheechobee, ca. 130 km to the south of this Hernando County population reported here. Paul Martin Brown reported the Hardee County population (Brown 2001), and a herbarium specimen collected by him on in April, 2001 was deposited in the University of South Florida Herbarium (http://florida.plantatlas.usf.edu/SpecimenDetails.aspx?PlantID=4127). The specimen is of a flowering shoot and the label indicates that the plant comprised a "well established colony of 100+ large clumps and many seedlings" and located in a "Bayhead near Little Charlie Creek and Peace River." A Bayhead is a seasonally wet plant community characterized by *Persea palustris, Myrica cerifera* L. and *Ilex cassine* L.

Phaius tankervilleae is native to China, Southeast Asia, to northern Australia and the Pacific (Gandawidjaja & Arditti 1982 and references therein), and is naturalized in the West Indies, Central and South America and Hawaii (Fowlie 1962). The nun's hood orchid was one of the earliest orchids introduced to cultivation (Holttum 1957).

Orchids rarely naturalize because of the lack of appropriate pollinators and mycorrhizal fungi needed for seed germination (Daehler 1998). *Phaius tankervilleae* has forms that are known to have both self-pollinating cliestogamous flowers, as well as potentially outcrossing chasmogamous flowers (Gandawidjaja & Arditti 1982). The self pollinating flowers may have promoted its widespread naturalization (Gandawidjaja & Arditti 1982). The chasmogamous flowers have been reported to be pollinated by carpenter bees (*Xylocopa*) (Van der Pijl & Dodson 1966), which are common in Florida. We don't know whether cleistogamous flowers occur in the Weeki Wachee or the Hardee County populations, or if the chasmogamous flowers are being pollinated by *Xylocopa* species or perhaps other bees. Bonnardeaux et al. (2007) found that an invasive *Disa* orchid in Australia was associated with more globally distributed mycorrhizae species than more narrowly distributed native orchids. This could also be the case with nun's hood orchid and could explain, in part, its ability to naturalize so widely. The seeds from the Wiki Wachee plants might also be able to use the mycorrhizae associated with other orchids (mentioned above) growing at the site. More research is needed to understand how this orchid has been able to naturalize in Florida, whereas the large numbers of other ornamental orchids cultivated in Florida have not. The nun's hood orchid is one of eleven species of orchids that have naturalized in Florida (Wunderlin & Hansen 2003; Pemberton et al. 2008).

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We thank Weeki Wachee State Park for allowing us to study *Phaius tankervilleae* in the park, and Paul Martin Brown for connecting the lead and corresponding authors, and facilitating, with the help of our co-authors, the documentation of the naturalization of the nun's hood orchid in central Florida. Elizabeth Yanza and Ivan Portilla are thanked for providing the Spanish abstract. William Mark Whitten and an anonymous reviewer gave us constructive and helpful reviews.

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BOOK NOTICES | BOOKS RECEIVED

Trees of Florida

Gil Nelson. 2011. **The Trees of Florida: A Reference and Field Guide, Second Edition.** (ISBN 978-1-56164-474-2, pbk.; 978-1-56164-475-9, pbk.). Pineapple Press, Inc., P.O. Box 3889, Sarasota, Florida 34230, U.S.A. (**Orders:** www.pineapplepress.com; 800-746-3275). $24.95 (hbk.), 428 pp., 170 line drawings, 150 color photos, 6" × 9".

From the Publisher: "This book is the first comprehensive guide to Florida's amazing variety of tree species: from scrub oak on the high central ridges to mangroves stretching along the southern coasts, from mighty live oaks to the delicate and diminutive hawthornes, from bald cypress with their knees poking up from the swamps to the coppery-colored gumbo limbo found in tropical hammocks of the Everglades and Keys, from the sabal palm found all over the state to the rare and endangered yew found only along the banks of the Apalachicola River in northern Florida. Florida, unique among the states, has both tropical and temperate forests. The early Florida visitor was awed by miles of unending pine flatwoods. Most modern Florida visitors are amazed by the lush tropical trees planted in cities, suburbs, and public gardens. This book covers both natives and exotics and includes suggested field sites for observing the species described."

1. Trees (Florida). **2.** Trees (Florida, Identification). **3.** Trees (Florida, Pictorial works).

Trees of Panama and Costa Rica

Richard Condit, Rolando Pérez, and Nefertaris Daguerre. 2011. **Trees of Panama and Costa Rica.** (ISBN 978-0-691-14707-9, hbk.; 978-0-691-14710-9, pbk.). Princeton University Press, 41 William Street, Princeton, New Jersey 08540, U.S.A. (**Orders:** press.princeton.edu/titles/9289.html). $85.00 (hbk.), $45.00 (pbk.), 552 pp., 438 color illus., 5 line illus., 482 maps, 6" × 9".

From the Publisher: "This is the first field guide dedicated to the diverse tree species of Panama and Costa Rica. Featuring close to 500 tropical tree species, *Trees of Panama and Costa Rica* includes superb color photos, abundant color distribution maps, and concise descriptions of key characteristics, making this guide readily accessible to botanists, biologists, and casual nature lovers alike."

1. Trees (Panama, Identification). **2.** Trees (Costa Rica, Identification).

Trees in Patagonia

Bernardo Gut. 2008. **Trees in Patagonia.** (ISBN 978-3-7643-8837-9, hbk.). Birkhäuser Verlag AG, P.O. Box 133, CH-4010, Basel, SWITZERLAND. (**Orders:** www.birdhauser.ch; www.springer.com/birkhauser/biosciences/book/978-3-7643-8837-9). $89.95, 283 pp., 760 illus. with 600 in color by Bernardo Gut, 7" × 10¼".

From the Publisher: "This book is a guide to the native trees and approximately 95% of the introduced arboreal species of Argentine and Chilean Patagonia. Introductory chapters convey an overview on what is termed 'Patagonia', as well as on the geology, climate, soils, and vegetation of Southern South America. Keys based on vegetative characters and richly illustrated descriptions of more than 170 species form the core of the manual. These chapters are followed by concise entries on afforestations, urban trees, and plantations of fruit trees in climatic enclaves. Renowned experts describe the most important National Parks of both Argentine and Chilean Patagonia. The last chapter is devoted to Carl Skottsberg and his remarkable expedition through Patagonia a hundred years ago."

Special collaboration Ing. Ftal. María Paula Guzzetti. Contributions by A. Díaz, P. Lépez, M. Rumboll, and G. Vittone.

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GOMPHRENA SERRATA (AMARANTHACEAE) NEW TO THE FLORA OF LOUISIANA

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ABSTRACT

Gomphrena serrata L. (Amaranthaceae) is reported as new to the Louisiana flora based on a specimen collected from Vernon Parish in the west central part of the state.

RESUMEN

Se cita *Gomphrena serrata* L. (Amaranthaceae) como nueva para la flora de Louisiana en base a un espécimen colectado en Vernon Parish en la parte centro-oeste del estado.

Prostrate globe amaranth, (*Gomphrena serrata* L.), an annual species in the Amaranthaceae is reported as new to the Louisiana flora. This species also has the common names of arrasa con todo and perpetua. Synonyms include *Gomphrena decumbens* Jacq. and *Gomphrena dispersa* Standl. Our specimens had fibrous roots, decumbent stems, heads narrower than 12 mm in diameter, and bractlets with narrowly cristate keels on some flowers as described as key characteristics for this species in the Flora of North America treatment by Clemants in 2003. Its range in the United States includes FL, GA, HI, MD, TX, and VA (Clemants 2003). Clemants (2003) also reports it from Puerto Rico, Virgin Islands, Mexico, Central America, and South America. It is not listed for Louisiana by Thomas and Allen (1996) but is mapped for Louisiana in the plants database (USDA NRCS 2011). The USDA NRCS listing for Louisiana is based on literature (Rollins 1981), but this is apparently erroneous since the Rollins work addresses members of Brassicaceae rather than Amaranthaceae. Therefore our collection is apparently the first for Louisiana. A duplicate of our collection was verified by Steve Clemants of the Brooklyn Botanic Gardens. The plant was probably introduced at the collection site which is a disturbed area. Associated species include *Croton capitatus* Michx., *Conyza canadensis* (L.) Cronq., and *Hypericum drummondii* (Grev. & Hook.) Torr. & A. Gray.

Voucher specimen: **LOUISIANA. Vernon Parish:** southern end of Range 40, N of LA 463 ca. 5 mi N of Pitkin, 31 Jul 2007, *Allen et al 20435* (BBG, BRIT, FTPK).

ACKNOWLEDGMENTS

We thank an anonymous reviewer for their helpful comments and suggestions.

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MACROTHELYPTERIS TORRESIANA (THELYPTERIDACEAE) NEW TO KENTUCKY

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ABSTRACT

Macrothelypteris torresiana is a non-native fern that has been expanding its range throughout the southeastern United States since 1904 and is here reported new to the flora of Kentucky. The habitat and associated flora of this population are discussed.

RESUMEN

Macrothelypteris torresiana es un helecho exótico que ha estado expandiendo su rango en el sureste de los Estados Unidos desde 1904 y se cita aquí nuevo para la flora de Kentucky. Se discute el hábitat y la flora asociada de esta población.

In November 2009, while collecting ferns for a class assignment the first and second authors collected a fern with unusually large fronds that did not fit any of the known fern species of Kentucky. Additional investigation revealed that the fern was *Macrothelypteris torresiana* (Gaudich.) Ching, an Asian species first collected outside of cultivation in the United States from Seminole County, Florida in May 1904 (Leonard 1972). Torres' fern, Mariana maiden fern, or swordfern has since spread throughout much of the southeastern United States and occurs from South Carolina to eastern Texas (Smith 1993; USDA, NRCS 2009). It continues to expand its range northward and has been recently reported from scattered locations in Tennessee (Beck & Van Horn 2007; McCoy 2008) and southwest Virginia (Wieboldt et al. 2011). Our collection represents the first report of this fern from Kentucky and is one of the northernmost known populations of *Macrothelypteris torresiana* in the United States.

Voucher Specimens: **KENTUCKY. Todd Co.:** S edge of Clifty, 0.6 km SE of the intersection of Kentucky 181 (Greenville Rd.) and Brown Rd., 0.2 km N of Brown Rd., disturbed mesic ravine, 10–15 m from edge of woods, elevation ca. 230 m, 36.98451°N, -87.14795°W, 21 Nov 2009, *C. Gorman 09-077 with M. Bruton and D. Greene* (ASPC, EKY, MO).

The Kentucky population was found in the Western Kentucky Coal Field region and consisted of about a dozen plants (Fig. 1). These occurred within a disturbed early-successional forest, in a mesic ravine underlain by Pennsylvanian sandstone. Associated flora included *Acer saccharum* Marsh., *Ailanthus altissima* (Mill.) Swingle, *Carpinus caroliniana* Walter, *Carya ovata* (Mill.) K. Koch, *Liriodendron tulipifera* L., *Lonicera japonica* Thunb., *Microstegium vimineum* (Trin.) A. Camus, *Persicaria longiseta* (Bruijn) Kitag., *Phegopteris hexagonoptera* (Michx.) Fée, *Phytolacca americana* L., *Polystichum acrostichoides* (Michx.) Schott, *Rubus argutus* Link, and *Sambucus canadensis* (L.) R. Bolli. It is not known how long *M. torresiana* has been present at this site; however, a return visit to the site in October 2010 indicated that the population appeared to remain stable compared to 2009. This population does not yet appear to be posing an imminent threat to native species, but considering this naturalized species has been reported as invasive elsewhere (Invasive Plant Atlas of the United States 2010); additional measures to monitor or eradicate this population may be justified. The record of this population has been submitted to EDDMapS (Early Detection and Distribution Mapping System), part of the Center for Invasive Species and Ecosystem Health (2010).

Previous treatments of the pteridophytes of Kentucky (Cranfill 1980; Jones 2005) did not include *Macrothelypteris torresiana*. Since this species can be successfully keyed to family in Jones (2005), we provide an updated key to the members of Thelypteridaceae for Kentucky.

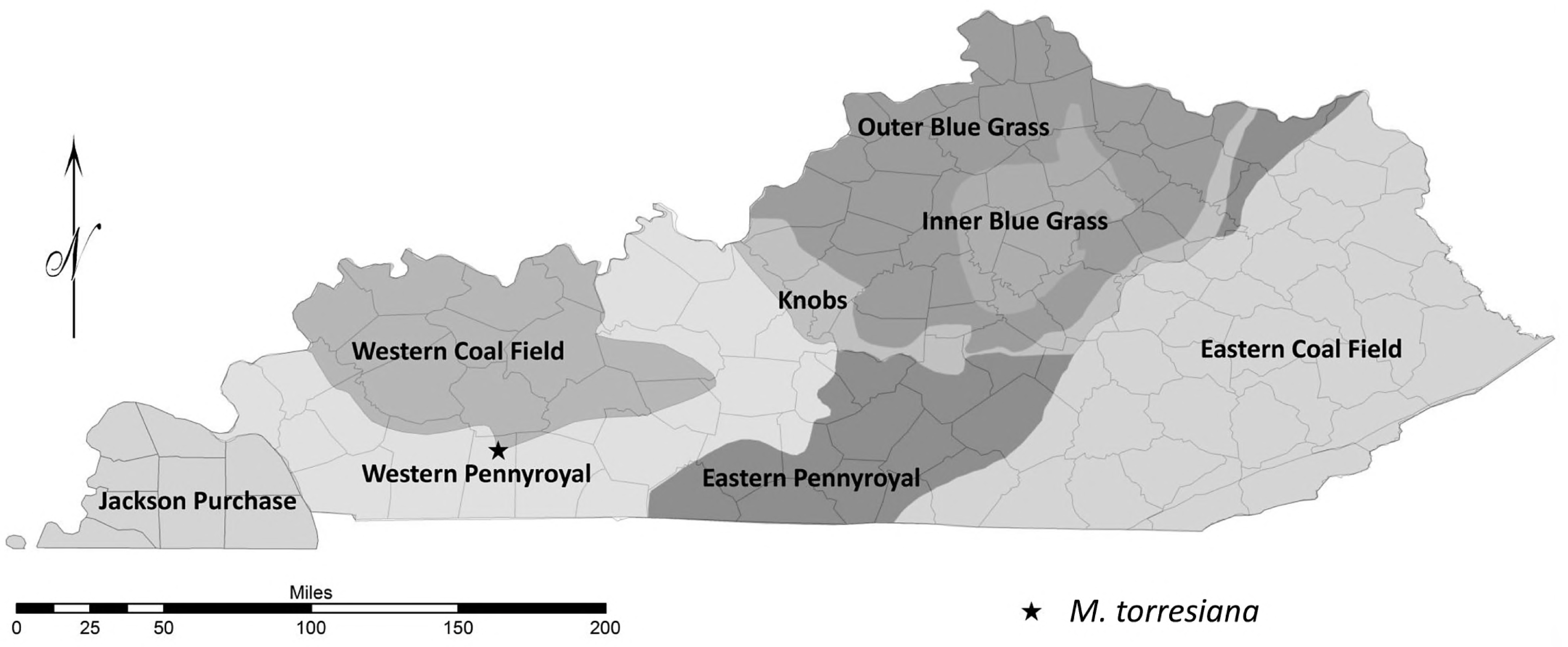

Fig. 1. Map showing *Macrothelypteris torresiana* occurrence relative to the physiographic regions of Kentucky.

KEY TO THE THELYPTERIDACEAE OF KENTUCKY

1. Blade narrowly elliptic to oblong, pinnate-pinnatifid; pinnae lanceolate-oblong with an adaxial groove present on the midribs; lowest pinnae to 1.6 cm wide.
   2. Pinnae tapering toward frond base (lower pinnae much reduced) ____ **Thelypteris noveboracensis**
   2. Pinnae not tapering toward frond base (lower pinnae well developed) ____ **Thelypteris palustris**
1. Blade strongly deltoid, bipinnatifid or bipinnate-pinnatifid; pinnae broadly lanceolate to lanceolate-ovate with midribs lacking an adaxial groove; lowest pinnae (1.7–)2–12 cm wide.
   3. Blade up to 60 cm in length; rachis with adnate wings ____ **Phegopteris hexagonoptera**
   3. Blade much larger, up to 200 cm; rachis naked ____ **Macrothelypteris torresiana**

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We would like to thank Ralph L. Thompson and Ronald L. Jones for reviewing the manuscript.

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HYPOCHAERIS MICROCEPHALA VAR. *ALBIFLORA* (*HYPOCHAERIS ALBIFLORA*: ASTERACEAE), NEW FOR THE VASCULAR FLORA OF MISSISSIPPI AND ITS DISTRIBUTION IN NORTH AMERICA

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ABSTRACT

Hypochaeris microcephala var. *albiflora* is newly reported to Mississippi. This South American native is vouchered in the United States only from Georgia, Louisiana, Mississippi, and Texas.

RESUMEN

Se reporta *Hypochaeris microcephala* var. *albiflora* nueva para Mississippi. La especie es nativa de America del Sur y en los Estados Unidos se conoce solamente de Georgia, Louisiana, Mississippi y Texas.

A few springs ago while botanizing for Plucheas near Bay St. Louis in Gulf Coastal Mississippi, I collected the South American native *Hypochaeris microcephala* var. *albiflora* (Kuntze) Cabrera (Compositae: *Cichorieae*). This taxon is typical of *Hypochaeris* by its plumose pappus bristles and paleate receptacles but is noteworthy among *Cichorieae* by having florets with white corollas. *Hypochaeris microcephala* var. *albiflora* was not reported for Mississippi in the statewide treatments by Lowe (1921) and Temple and Pullen (1968). The treatments by Cronquist (1980) and Bogler (2006) do not list *H. microcephala* var. *albiflora* for Mississippi. Neither the McCook and Kartesz (2010) nor the USDA-NRCS (2010) websites list *H. microcephala* var. *albiflora* for Mississippi, and it is not listed in recent floras in the southern part of the state (e.g., Alford 2001). Thus, it appears that *H. microcephala* var. *albiflora* is a new report for the vascular flora of Mississippi. The purpose of this note is to voucher *H. microcephala* var. *albiflora* in Mississippi, to give a quick overview of this taxon, and to track the range expansion of this invasive weed in North America. *Hypochaeris microcephala* (Sch. Bip.) Cabrera var. *microcephala*, a different taxon, is a yellow-flowered South American endemic.

Hypochaeris microcephala var. *albiflora* (sub the orthographic variant "*Hypochoeris*") was reported by Shinners (1966) as new to North America from material collected within five miles of the Sabine River in Orange County, Texas. Shortly thereafter, Thieret (1969) reported *H. microcephala* var. *albiflora* as new to Louisiana. The range in the United States of *H. microcephala* var. *albiflora* was given by Cronquist (1980) as Louisiana and Texas. Correll and Johnston (1970) treated *H. microcephala* var. *albiflora* as only in Orange County and as the only member of the genus in Texas, but soon thereafter Tomb (1974) provided an illustration of *H. microcephala* var. *albiflora*, cited it in four Texan counties, and reported an additional two species of *Hypochaeris* for Texas. Because the report by Tomb (1974) so quickly followed Correll and Johnston (1970), this suggests that species of *Hypochaeris* are overlooked and/or expanding their ranges.

The dot-map of *H. microcephala* var. *albiflora* (sub the binomial *H. microcephala*) in Texas by Turner et al. (2003) shows it to occur in 13 counties, all in southeastern Texas. The dot-map of *H. microcephala* var. *albiflora* in Louisiana by Gandhi and Thomas (1989) shows it in eight parishes and seven years later Thomas and Allen (1996) plot it in 13 parishes. Study at the Tulane University herbarium in May 2010 showed that *H. microcephala* var. *albiflora* is known in Louisiana also from East Baton Rouge and Tangipahoa Parishes. Both Gandhi and Thomas (1989) and Thomas and Allen (1996) report it in St. Tammany Parish, so the report herein of this taxon in adjacent Hancock County on the Mississippi Gulf Coast is not fully unexpected.

Carter et al. (2009) report a noteworthy eastward leap of *H. microcephala* var. *albiflora* into coastal Georgia,

not too far north of Jacksonville, Florida. Although *H. microcephala* var. *albiflora* is reported in Georgia and Mississippi from collections made in 2008, it seems possible that it was present in Georgia and Mississippi earlier than 2008, considering that it has become increasingly more frequent in Texas and Louisiana. That said, I suspect this invasive weed has been or will soon be collected along the Gulf Coast in intermediate Alabama and in Florida as well. Tyrl et al. (2009) and the Oklahoma Vascular Plants Database (2010) do not list *H. microcephala* var. *albiflora* in Oklahoma, thus the report of it in Oklahoma by Bogler (2006) cannot be verified and seems erroneous. In summary, *H. microcephala* var. *albiflora* is known to me in the United States from only Georgia, Louisiana, Mississippi, and Texas, is expected in Alabama and Florida, and in the past five decades has spread mostly eastward to the Atlantic Coast of Georgia from Orange County, Texas in the Sabine River basin, where it was reported as new to North America by Shinners (1966).

Although Azevêdo-Gonçalves & Matzenbenbacher (2005) believe that *H. microcephala* is a hybrid and validate the binomial *H. albiflora* (Kuntze) Azevêdo-Gonç. & Matzenb., for stability sake and because in general I do not have full confidence in name applications in *Hypochaeris*, I prefer to apply the familiar trinomial *H. microcephala* var. *albiflora* to our taxon as in Cronquist (1980), Tomb (1974), etc. As suggested by Azevêdo-Gonçalves & Matzenbenbacher (2005), this taxon may deserve recognition at the species rank, but I think it is unwise at present to introduce a new name for it into North American literature. Additionally, I am somewhat concerned that a pre-2005 binomial may be available for this *Hypochaeris*, perhaps masquerading elsewhere in synonymy.

Hypochaeris microcephala var. *albiflora,* at least as it occurs and is circumscribed in the United States (e.g., Cronquist 1980), is similar to *H. chillensis* (Kunth) Britton by stems leafy proximally and uniseriate pappus, but differs by pinnatifid (vs. merely dentate) basal leaves, white (vs. yellow) corollas, never hispid (vs. sparsely hispid) outer phyllaries, and usually by smaller capitula. Synonyms of *H. chillensis* in Cabrera (1978) include *H. brasiliensis* (Less.) Benth. & Hook. f. ex Griseb. and *H. tweediei* (Hook. & Arn.) Cabrera, names used, respectively, by Cronquist (1980) and Shinners (1966). The nomenclature, typology, and representative specimen citations of our white-flowered *Hypochaeris* are cited below.

Hypochaeris microcephala var. **albiflora** (Kuntze) Cabrera, Notas Mus. La Plata, Bot. 2:201. 1937. (**Fig. 1**). *Hypochaeris brasiliensis* var. *albiflora* Kuntze, Revis. Gen. Pl. 3(3):159. 1898. *Hypochaeris albiflora* (Kuntze) Azevêdo-Gonç. & Matzenb., Compositae Newslett. 42:3. 2005. Syntypes: ARGENTINA. Santa Fe: Ceras, Oct 1892, *Kuntze s.n.* (NY); Paraguay: Concepcion, Sep 1892, *Kuntze s.n.* (NY).

Distribution.—Native to southern South America (Argentina, Brazil, Paraguay, and Uruguay). Unknown in Mexico, Central America, and the West Indies. Naturalized in eastern Australia (Auld & Medd 1987; Richardson et al. 2003). Naturalized in the United States (Georgia, Louisiana, Mississippi, Texas; reported in Oklahoma, perhaps erroneously so, and its occurrence there not verified by me; and expected in Alabama and Florida) where this knee-high scurfy invasive weed flowers from February to June with a peak in April and May.

Representative specimens (1 collection per state): **GEORGIA. Camden Co.:** US Hwy. 17, N of Kingsland, just N of jct. US Hwy. 17 and Daisy Ave, just S of jct. US Hwy. 17 and Kinlaw Road, 30.85883°N 81.70219°W, 30 Apr 2008, *Carter & Baker 18369* (MO, VSC [photo MO]). **LOUISIANA: St. Tammany Parish:** abundant lawn weed at Harold Marcho's house at 1315 Kings Roe in Pine Hurst subdivision, immediately NE of I-10 jct. with LA Hwy. 433 in Slidell, 30°15'09"N, 89°45'23"W, elev. 7 ft, 13 May 2010, *Pruski & Marcho 4586* (LSU, MO, NO). **MISSISSIPPI. Hancock Co.:** open sandy pine woods roadside on Chazel Lane on N bank of Jordan River, 0.7 mi NW of where MS Hwy. 43-603 crosses the Jordan River, 1.5 mi SW of Kiln, 9 mi N of Gulf of Mexico, 30°23'30"N, 89°27'03"W, elev. 13 ft, 14 May 2008, *Pruski 4326* (BRIT, MO, USMS). **TEXAS. Orange Co.:** 6 mi N of Orange on state Hwy. 87 from north-side jct. with I-10, 17 May 1966, *Shinners 31370* (MO).

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I would like to thank Rosa Ortiz (MO) for translating into Spanish the abstract; and Anne Bradburn (NO) and Steven Darwin (NO) for help during my studies in the Tulane University herbarium. I thank Charles Bryson, Richard Carter, and an anonymous reviewer for helpful suggestions and improvements.

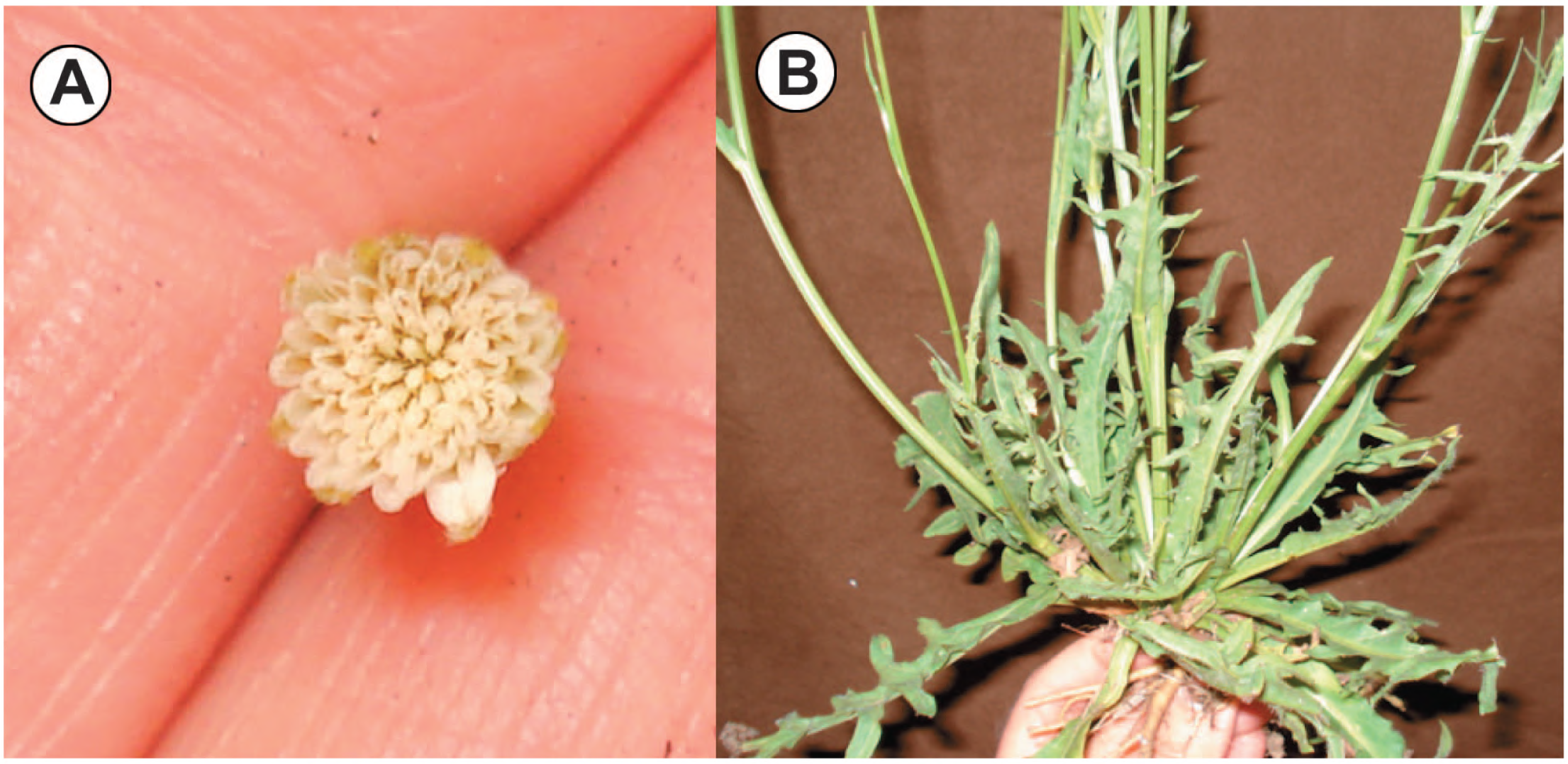

Fig. 1. *Hypochaeris microcephala* var. *albiflora* (Kuntze) Cabrera. A. Capitulum showing the white corollas. B. Plant base showing pinnatifid basal and proximal cauline leaves. (Both from *Pruski & Marcho 4586*).

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CRATAEGUS CHRYSOCARPA VAR. *DODGEI* (ROSACEAE) NEW TO NORTH CAROLINA

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ABSTRACT

Crataegus chrysocarpa var. *dodgei* (Rosaceae) is reported for the first time from North Carolina. This hawthorn is an enigmatic variety that has alternatively been given specific status (*C. dodgei*). A brief statement of the taxonomic interpretation and biogeographic significance of this taxon is provided.

RESUMEN

Se cita *Crataegus chrysocarpa* var. *dodgei* (Rosaceae) por primera vez de Carolina del Norte. Este espino es una variedad de difícil comprensión a la que se ha dado alternativamente un status específico (*C. dodgei*). Se aporta una breve exposición de su interpretación taxonómica y significado biogeográfico de este taxon.

In North America, *Crataegus chrysocarpa* Ashe [series *Rotundifoliae* (Eggleston ex Sargent) Rehder] is a widespread, but primarily boreal taxon found in northern regions of the continent (USDA, NRCS 2011). When broadly interpreted as the core species of a complex of closely related hawthorns, the composite range extends from the Pacific Northwest across southern Canada and adjacent states of the U.S. to the Atlantic, with southern extensions in the Rocky Mountain Region to central Colorado and recently attributed to New Mexico (Legler 2010), and also in the Appalachians to West Virginia, Virginia, and now North Carolina. In congruence with this broad distribution pattern, numerous varieties have been attributed to this polymorphic species and these varieties have in turn been variously interpreted as independent taxa (e.g., Palmer 1937, 1950, 1952; Kruschke 1965; Smith & Phipps 1987; Phipps & O'Kennon 2004).

One eastern relative of *C. chrysocarpa* that has received alternative specific and varietal treatment is *C. dodgei* Ashe. We have chosen to follow the early taxonomy of Palmer (1937), relegating this taxon to varietal status inclusive within the *C. chrysocarpa* species complex. Rationale behind this opinion is based on observance of unstable morphological characters used to distinguish *dodgei* from other eastern entities of the *chrysocarpa* complex. Specifically, the range of marginal lobing in the leaves of *dodgei*, which is one of the most important characters used in the separation of *dodgei* (Palmer 1950, 1952; Smith & Phipps 1987) varies from obscure to obtuse (typical) to acute (most similar to other *chrysocarpa* entities). The North Carolina *dodgei* plants exhibit distinctly acute leaf lobes, which puts them on the more extreme end of resemblance to other eastern varieties of *chrysocarpa*. Considering *dodgei* as a variety of a species complex that encompasses a wide range of intergradation is a simplifying approach, though arguments for specific recognition exist, as well. It should be noted that Palmer changed his recognition of *dodgei* from a variety to species level in 1950. It is not the purpose or intent of this paper to define or revise any new taxonomic rank for *dodgei*, but merely to document its presence in North Carolina.

Crataegus chrysocarpa Ashe var. **dodgei** (Ashe) Palmer (syn. *Crataegus dodgei* Ashe)—This is the only member of the *chrysocarpa*-complex known to reach southeastern U.S. states, where it was previously recorded only as far south as Grayson County, Virginia (Wieboldt et al. 2011). The significance of our collections is that they represent a new southernmost station for this taxon. Likewise, this documentation is a state record

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for North Carolina, but not a surprising find considering the nearest population is only ca. 15 km northeast across the North Carolina/Virginia state line. Previous documentation of this plant for the state (Weakley 2010) hinged upon a single dubious tree in Ashe County (e.g., *D.B. Poindexter 09-1079* [BOON]) of possible hybrid origin. Due to the ambiguity of this Ashe County plant, the following specimens are cited as reliable documentation of this taxon from North Carolina.

Voucher specimens: **NORTH CAROLINA. Alleghany Co.:** Gap Civil Township, Edwards Crossroads, located along Bald Knob Rd. (SR 1416) at Bald Knob, accessed via the Edwards property, growing in the edge of a pasture on the W side of the mountain at 36°33'11.03"N, 81°6'20.88"W, 1016 m, 7 Aug 2008, *D.B. Poindexter 08-726* (BOON); same locality, 4 Sep 2009, *D.B. Poindexter 09-1030* (BOON, NCU); 6 May 2010, *D.B. Poindexter & R.W. Lance 10-141* (BOON, NCU).

The observed population was small, consisting of approximately 15 individuals that were utilizing open woodland margins and adjacent pasture for habitat. This environment differs substantially from the nearest Virginia population that occurs along the banks of the New River (*A.M. Harvill, Jr. 37522* [FARM]).

The uniform morphology of these trees substantiates the validity of this identification and the undeniable presence of this taxon in North Carolina. Syntopic with this population is *Crataegus macrosperma* Ashe [series *Tenuifoliae* (Beadle ex Sarg.) Rehder], and interestingly, one tree at this locality exhibited mixed characteristics suggestive of an interserial hybrid between *C. chrysocarpa* var. *dodgei* and *C. macrosperma* (e.g., *D.B. Poindexter and R.W. Lance 10-143* [BOON]).

Due to the small size of this population and the lack of any additional known localities within the state, this taxon should be monitored.

ACKNOWLEDGMENTS

The first author would like to express gratitude to the various donors associated with Roaring Gap Club for their financial support. These contributions have facilitated not only a floristic inventory of Alleghany County, NC, but consequential new discoveries such as this that broaden our understanding of plant biogeographical patterns.

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LLAVEA CORDIFOLIA (PTERIDACEAE), NEW FOR TEXAS AND THE UNITED STATES

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ABSTRACT

Llavea cordifolia (Pteridaceae) is reported as new to the Texas flora and to the flora of the United States.

RESUMEN

Llavea cordifolia (Pteridaceae) se cita como nueva para la flora de Texas y para la flora de los Estados Unidos.

Llavea is a morphologically distinctive, monotypic genus previously known to occur primarily in the mountains of Mexico from Coahuila, Nuevo León, and Tamaulipas south to Chiapas, but also in Guatemala and Costa Rica (Stolze 1981; Mickel & Beitel 1988; Lellinger 1989; Jaramillo et al. 2000; Mickel & Smith 2004). It has not previously been reported from Texas (e.g., Correll & Johnston 1970; Hatch et al. 1990; Jones et al. 1997; Yarborough & Powell 2002; Diggs et al. 2006) or from the United States (Windham 1993 [Flora North America]; Kartesz 1999; USDA Plants 2011).

The evolutionary relationships of the genus have been unclear—Copeland (1947) considered it to be derived from *Pellaea*, Pichi Sermolli (1963) placed it with *Cryptogramma* and *Onychium*, while Tryon and Tryon (1982) suggested there was a distant relationship to *Lygodium*. Family placement has ranged from Adiantaceae to Cryptogrammaceae (e.g., Smith et al. 2006), Llaveaceae, and Pteridaceae. Recent molecular research (e.g., Schuettpelz et al. 2007; Schuettpelz & Pryer 2007, 2008) has shown it to be in the Pteridaceae in a cryptogammoid clade consisting of three genera including *Cryptogramma* (6–11species of North America, South America, Europe, and Asia) and *Coniogramme* (an Old World genus). This cryptogammoid clade is the most basal of the five clades comprising the Pteridaceae, making *Llavea* only distantly related to other members of that family. Schuettpelz et al. (2007) noted regarding this clade, "The morphology is highly variable in this group, and a clear morphological synapomorphy is lacking. Although all three genera display sterile-fertile leaf dimorphism, this character is widespread throughout the Pteridaceae." *Llavea* has long been cultivated as an ornamental—Hooker (1860) pointed out that it was "one of the most beautiful, and, in a state of cultivation, rarest of ferns, native of Mexico, with a very peculiar habit…. No fern-collection suitable to a warm greenhouse should be without this charming plant."

A collection from Presidio County, Texas is apparently the first documented occurrence of this species for both Texas and the United States.

Voucher specimen: **TEXAS. Presidio Co.:** moist limestone bluff, 1108 m (3635 ft), Big Bend Ranch State Park, ca. 11.1 km (6.9 mi) from the U.S.-Mexico border, 10 May 1992, *R.J. O'Kennon & B.H. Warnock 10570* (BRIT).

While the Texas collection of this species was made in 1992, at that time it was thought to be an aberrant individual of an *Osmunda* species. The specimen remained in storage until late 2010 when its identity was realized. In Mexico, it occurs on rocky slopes of moist woods and cliffs (Mickel & Smith 2004). Tryon and Tryon (1982) noted, "*Llavea* grows in mesic canyons, or other rocky places in pine and oak woods, or in tropical forests. Sometimes it occurs on roadsides, on rock walls or in damp soil. It is principally, perhaps always, a calciophile." It superficially somewhat resembles *Osmunda regalis*, ROYAL FERN, but is quite different in appearance from all other Texas species. The current status of the species in Texas is unknown. However,

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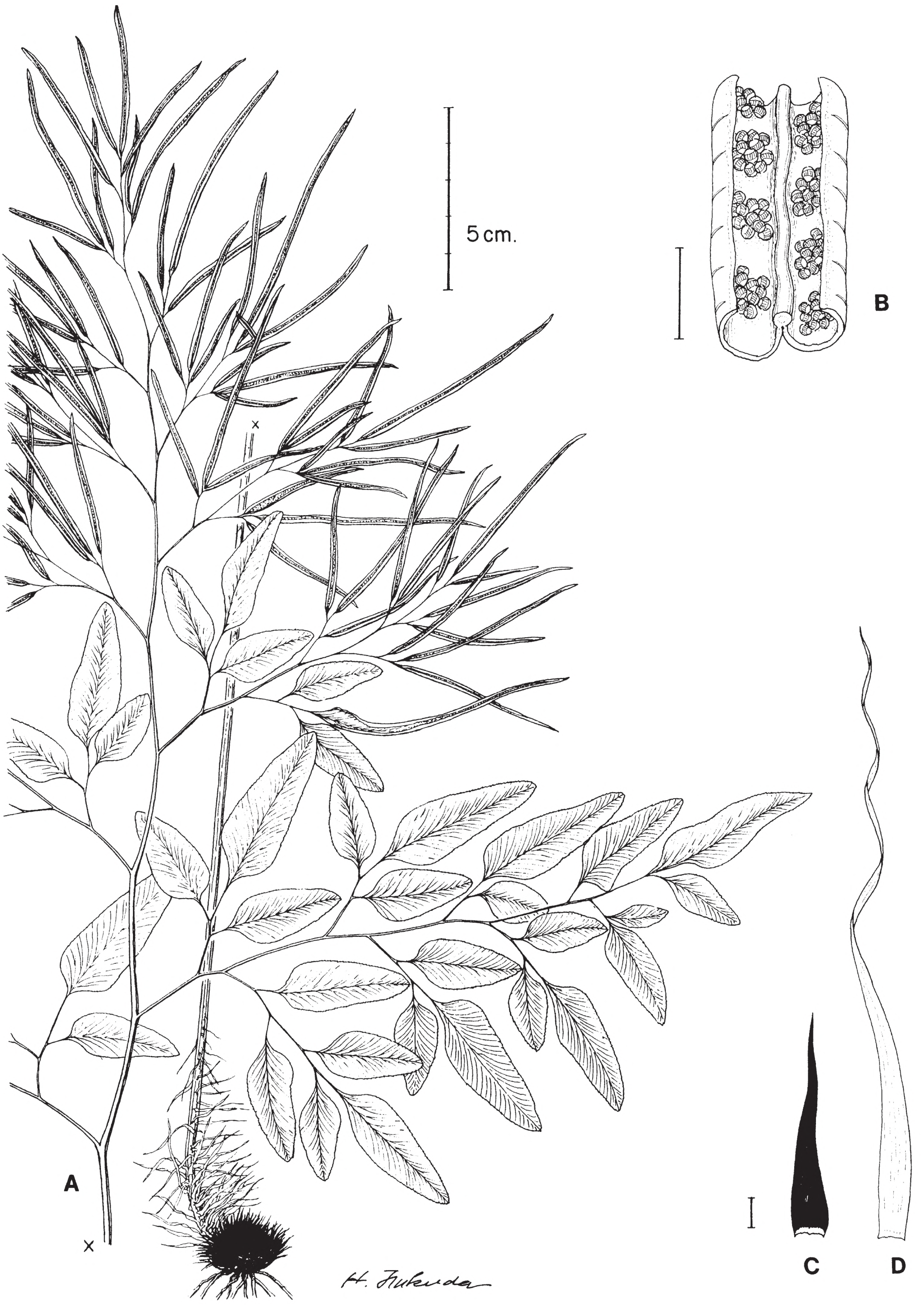

Fig. 1. Line drawing of *Llavea cordifolia* (reprinted with permission from Mickel & Smith 2004, fig. 174).

Fig. 2. Scan of Texas voucher specimen of *Llavea cordifolia (O'Kennon & Warnock 10570*, BRIT*).*

because it is known in this country from only a single station in Presidio County, we consider this species to be of conservation concern in both Texas and the United States.

Llavea cordifolia can be recognized by the following description (modified from Stolze 1981; Mickel & Beitel 1988; Pacheco 1995, and Mickel & Smith 2004) and from Figures 1 and 2.

Llavea cordifolia Lag., LLAVE´S FERN, CORDATE-LEAVED LLAVEA, HELECHO DE LA LLAVE. Plants terrestrial or on rocks; rhizomes typically horizontal or nearly so, compact, 2–2.5 cm diam., with scales linear-lanceolate, 0.6–1.4 cm long, entire, blackish; leaves clumped, 0.45–1.2(–1.47) m long, partially dimorphic (fertile leaves similar to sterile except with much narrower, longer sporangia-bearing pinnae limited to the terminal 1/3 of the blades); petioles ca. equal in length to blade, grooved, glabrous except for large (1–3 cm long), yellowish, linear-lanceolate scales near base; leaf blades broadly ovate, mostly 3-pinnate basally, 2-pinnate apically, subcoriaceous, glabrous, with ultimate segments distinctly stalked, with veins 1–2 forked, free, extending to segment margins, the ends prominent; sterile segments ovate-deltate, 2–3 cm long, 0.8–2.2 cm wide, grayish-green, marginally serrulate; fertile segments much narrower, linear, 2.5–8.5 cm long, 1–4(–5) mm wide, with inrolled margins partially covering sori; sori borne along the veins, so abundant as to often essentially cover the entire abaxial surface of the segments; indusium differentiated, with short glandular hairs on inside; $n = 29$ (Tryon & Tryon 1982; Mickel & Smith 2004). [*Allosorus karwinskii* Kunze, *Botryogramme karwinskii* (Kunze) Fée, *Ceratodactylis osmundoides* J. Sm.] The sole U.S. collection was sporulating on 10 May.

This species can be instantly distinguished from all other Pteridaceae and indeed all other ferns in the Trans-Pecos and Texas by the combination its large, striking, partially dimorphic leaves (fertile leaves similar to sterile except with much narrower, longer fertile pinnae limited to the terminal 1/3 of the blades) and the contrast between the blackish rhizome scales and the yellowish scales at the bases of the petioles.

ACKNOWLEDGMENTS

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Moss Flora of Central America

Bruce Allen. Contributons from Ronald A. Pursell and Robert R. Ireland. 2010. **Moss Flora of Central America. Part 3. Anomodontaceae–Symphyodontaceae.** (ISBN 978-930723-95-5, hbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 117 (ISSN 0161-1542). Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $110.00, 732 pp., illus., 7" × 10" .

From the Publisher: The Moss Flora of Central America is a four-part, revisionary flora. Parts 1 and 2, published in 1994 and 2002, respectively, treated a total of 521 species. The newly published Part 3 gives keys, descriptions, and discussions for 239 moss species. In addition, for each species precise type information is provided; distribution within Central America is documented by the examination of specimens; world distribution is indicated; habitat notes based on personal field experience or taken from collection labels are provided; and a list of previously published illustrations is given. Beginning with Part 2, all species included in the Flora are illustrated by means of black-and-white line drawings. Part 3 contains numerous genera that treat all tropical American species of those genera, as well as major treatments on *Lepidopilum* (18 species), *Thamniopsis* (13 species), *Pireella* (11 species), and *Porotrichum* (11 species); it will likely prove useful for many genera throughout the Neotropics. Work is underway on Part 4 of the Flora, which will treat 213 species; when completed, the Flora will treat approximately 973 moss species.

Flora of Costa Rica

B.E. Hammel, M.H. Grayum, C. Herrera y N. Zamora, eds. Silvia Troyo, Illustrations. 2010. **Manual de Plantas de Costa Rica. Volumen V. Dicotiledóneas (Clusiaceae–Gunneraceae).** (ISBN 978-935641-01-8, hbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 119 (ISSN 0161-1542). Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $125.00, 970 pp., 412 line drawings, 30 b/w photos, 8 color plates, 7" × 10".

From the Publisher: "Costa Rica, lying between Nicaragua and Panama and thus centered in isthmian Central America—a biogeographical funnel between South and North America, densely rich in species and geological history—is also one of the few tropical countries to have an accurate, up-to-date, specialist- and specimen-based count of its known flora. Intensive and continuing exploration over the last 25 years has resulted in a large increase in the number of new species. Currently, more than 9,700 species of native or naturalized vascular plants (including a few commercially cultivated exotics) are known from the country. The *Manual de Plantas de Costa Rica* is a series of illustrated identification manuals, providing the general public, students, and scientists alike with the most current, basic, and critical information on the largest subgroup of those, the seed plants. The work will be published in seven volumes and includes a general introductory volume in English and Spanish. The Manual is the first comprehensive Spanish-language account of the Costa Rican flora."

This is another magnificent volume of an ongoing tropical flora from the Missouri Botanical Garden. I can't imagine anyone being disappointed with owning a copy!—*Barney Lipscomb, Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107-3400, U.S.A.*

Symposium Proceedings

Bruce E. Ponman and James S. Miller, eds. 2011. **Realizing Nature's Potential: Proceedings of the William L. Brown Symposium Honoring Dr. Gordon Cragg.** (ISBN 978-930723-96-2, pbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 118 (ISSN 0161-1542). Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $35.00, 196 pp., illus., 7" × 10".

From the Publisher: Realizing Nature`s Potential: The Once and Future King of Drug Discovery was a two-day event held at the Missouri Botanical Garden in the fall of 2006 in honor of Dr. Gordon Cragg. Dr. Cragg, former chief of the Natural Products Branch of the National Cancer Institute, was throughout his career a tireless advocate for the conservation of nature in order to maintain the rich chemical diversity that has so often been vital to the development of new pharmaceuticals.

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A FLORISTIC INVENTORY OF GRAND TETON NATIONAL PARK, PINYON PEAK HIGHLANDS, AND VICINITY, WYOMING, U.S.A.

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ABSTRACT

Federal lands totaling 766 mi^2 (198,393 ha) of Grand Teton National Park, the John D. Rockefeller Jr. Memorial Parkway, Bridger-Teton National Forest (Pinyon Peak Highlands), and Targhee National Forest (Wyoming's northern portion) were inventoried. Collected were 8,002 vouchers of vascular plants at 375 locations. They represent 962 unique taxa (904 species) in 347 genera and 86 families. For the Park and Parkway proper, the relevant numbers are 909 unique taxa (861 species, 42 infraspecies, and 6 hybrids); 112 of which are new records. One escaped ornamental was documented as new to the State. Species of conservation concern (Wyoming Natural Diversity Database) totaled 42. Exotics to North America (72 unique taxa) represented 7.5 percent of the flora, a relatively low number when compared to similar inventories in Wyoming.

RESUMEN

Fueron inventariados territorios Federales que totalizan 766 millas cuadradas (198,393 ha) del Grand Teton National Park, el John D. Rockefeller Jr. Memorial Parkway, Bridger-Teton National Forest (Pinyon Peak Highlands), y Targhee National Forest (porción norte de Wyoming). Se colectaron 8,002 testigos de plantas vasculares en 375 localizaciones. Estos representan 962 taxa únicos (904 especies) de 347 géneros y 86 familias. Para el Park y Parkway propiamente dicho, los números son 909 taxa únicos (861 especies, 42 taxa infraespecíficos, 6 híbridos); 112 de los cuales son nuevas citas. Se citó una ornamental escapada nueva para el estado. Las especies protegidas (Wyoming Natural Diversity Database) fueron 42. Exóticas para Norte América (72 taxa únicos) representaron el 7.5 por ciento de la flora, un número relativamente bajo cuando se compara con inventarios similares de Wyoming.

INTRODUCTION

This contribution discusses a broad-scale inventory of the vascular plants documented on federal lands of the southern Greater Yellowstone Ecosystem. The areas are: Grand Teton National Park (Park), the John D. Rockefeller Jr. Memorial Parkway (Parkway), the northern-most portion of Targhee National Forest (Targhee) in Wyoming, and a remote segment of the Bridger-Teton National Forest (Highlands). This region is known for its lack of human developments and its wild character. Inventories had been conducted on lands adjacent to the current one: the Southwest Absarokas (Snow 1989); the Targhee National Forest (Markow 1994); and the Gros Ventres and Mount Leidy Highlands (Hartman 1996; Lichvar 1979).

This botanical inventory is part of the larger effort by the Rocky Mountain Herbarium (RM) to produce a critical flora of the Rocky Mountains and to map, based on vouchered specimen, the distributions of its taxa in relatively fine detail (Hartman 1992; Hartman & Nelson 2008; Hartman et al. 2009; Reif et al. 2009). To this end, over 64 (48 as Master's degree projects) major floristic inventories have been conducted during the past 32 years in Arizona, Colorado, Idaho, Kansas, Montana, Nebraska, New Mexico, Oregon, South Dakota, Utah, Washington, and Wyoming. Over 600,000 new numbered collections have been obtained by graduate students, staff, and research associates of the RM. These specimens form the core of the Rocky Mountain Herbarium plant specimen database (700,000+ specimen record, 25,000+ specimen images) (Hartman et al. 2009).

Study area.—The lands surveyed lie in the Greater Yellowstone Ecosystem of northwest Wyoming, wholly within Teton County (Figure 1). They belong to the Middle Rocky Mountain Province (Horberg 1938).

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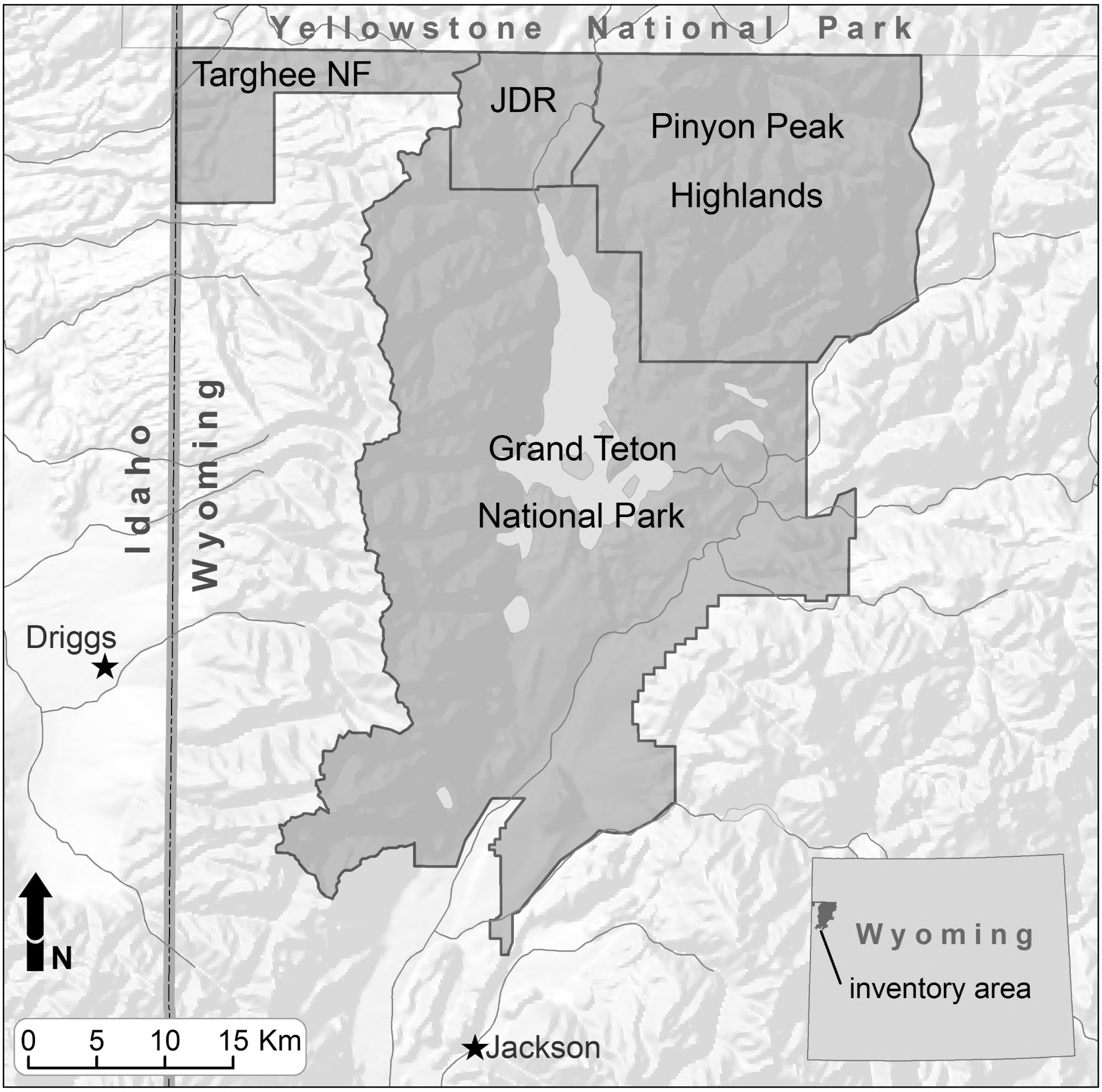

Fig. 1. Boundaries of the federal lands included in the floristic inventory: Grand Teton National Park, John D. Rockefeller Jr. Memorial Parkway, Bridger-Teton National Forest (Pinyon Peak Highlands), and a portion of the Targhee National Forest, Wyoming. The area is located in extreme northwest Wyoming, just south of Yellowstone National Park.

The unique geology and associated topography coupled with three converging floristic regions (Rocky Mountain, Great Basin, and northern Great Plains) yield a highly diverse flora.

The National Park Service administers the bulk of the lands. Grand Teton National Park and the John D. Rockefeller Jr. Memorial Parkway total 521 mi^2 (134,938 ha). To the east, the contiguous western portion of the Teton Wilderness, Bridger-Teton National Forest, consists of 194 mi^2 (50,246 ha). Finally, the Wyoming section of the Targhee National Forest, immediately west of the Parkway, totals 51 mi^2 (13,209 ha). Thus, the inventory covered 766 mi^2 (490,240 acres; 198,393 ha) of public lands.

Boundaries.—The western boundary is along the Teton Divide, from near Jackson Hole Mountain Resort on the south to the Parkway (Figure 1). It continues west to Indian Lake on the Targhee, north to the southern edge of Yellowstone National Park, and east to Gravel Creek, in the Pinyon Peak Highlands. The eastern delineation follows Pacific Creek southward to and along the eastern edge of the Park. On the

south, it extends west (four miles north of Jackson) where it completes the loop at the Resort. The area lies between approximately N44°07' and N43°32' latitude, north and south, respectively; likewise W110°25' and W111°01' longitude, east and west.

Topography.—The Teton landscape is nothing short of spectacular. The range rises abruptly from the valley floor (Jackson Hole) with a maximum relief of 6,772 feet (2,064 m). Glaciers and permanent snowfields occur on north and east exposures at high elevations. The Grand Teton rises to an elevation of 13,770 feet (4,197 m) with associated peaks extending to the north and south, along the Teton Divide, for a total distance of 40 miles (64 km).

In contrast, rolling hills and abundant wetlands characterize the Targhee (west of the Parkway). These wetlands, perpetuated by groundwater discharge and general runoff, are often extensive and complex in structure. The floating peat mats and ephemeral ponds provided novel habitats.

The Parkway bridges the northern slope of the Teton Range and the Yellowstone Plateau. It contains extensive wetlands including thermal springs and pools. A rolling topography dissected by the Snake River contributes to the landscape.

The Pinyon Peak Highlands lie east of the Parkway and the Park. Some shared features are porous volcanic soils and rolling terrain. The remote region is indeed a "perched highlands" with its namesake Pinyon Peak (9,705 feet; 2,958 m) (Whitlock 1993; Love et al. 2003). Although mostly montane, a number of scattered peaks provide subalpine environments. The Highlands drain to the south and then into Jackson Hole. Much of the Teton Wilderness was burned by "The Yellowstone Fire" of 1988 (Christensen et al. 1989).

Lowest in elevation is Jackson Hole, a flat valley dominated by sagebrush. It is the downthrown block of the Teton Fault that gave rise to the Tetons (Love et al. 2003). It ranges in elevation from 6,354 to 6,772 feet (1,937–2,064 m). The Snake River bisects Jackson Hole creating braided channels with oxbow ponds. Many of the lakes were formed by glaciers descending from the Yellowstone plateau or the Tetons near the end of the Pleistocene (Love et al. 2003).

Climate.—Reliable long-term weather data are from the Moose, Moran, and Snake River weather stations (Curtis & Grimes 2004). Average daily high and low temperatures for the Moran station, centrally located and most representative of the area, are 69 and 37, 79 and 42, and 78 and 40° F for June, July and August, respectively (21 and 3, 26 and 6, 26 and 4° C) (HPRCC 2010). From 1933 through 2002, the highest recorded temperature was 97° F (36° C) at Moose while the lowest recorded temperature was -63° F (-53° C) at Moran. The extreme northwest corner of Wyoming is generally the coldest. The high latitude and high elevation makes it subject to the passage of cold polar air masses (Dirks & Martner 1982). As a consequence, cold air becomes trapped in the valleys and radiative heat loss from snow-covered surfaces increases winter cooling (Dirks & Martner 1982). Average summer frost-free periods are short: 14 days at Moran, 29 days at Moose (Becker et al. 1961).

Most precipitation falls as snow (Knight 1994). Estimated annual snowfall at higher elevations ranges from 200 to 500 inches (508–1,270 cm) (Farnes 1974). In the Tetons, melt water flows from alpine snowpacks throughout the summer. Summer brings the dry period with average rains totaling a mere 4.12 inches (10.5 cm) for June, July, and August at Moran (period 1911–2010) (HPRCC 2010). A predominant west to southwest flow of air delivers both winds and thunderstorms in the summer. This is also true of frontal winds in winter (Curtis & Grimes 2004), although they may range from north to south.

Geology and geomorphology.—The greater Teton landscape is the result of three regional mountain-building phases. First, the Sevier Orogeny of the Cretaceous caused widespread compression of the Rocky Mountain region (Love et al. 2003). Thus, sedimentary strata were pushed eastward to the southern Tetons as evidenced by the Teton-Gros Ventre uplift. Second, and partially concurrent, was the Laramide Orogeny that began in late Cretaceous (70 mya). It led to the first significant uplift of the Tetons, again due to compression. Thrust activity along the Buck Mountain, Cache Creek, and Forellen Peak faults elevated the basement Precambrian. These include the Mount Owen Granite, Webb Canyon Gneiss, and Rendezvous Metagabbro, some of the oldest rocks in Wyoming with an estimated age of 2.68 billion years (Love et al.

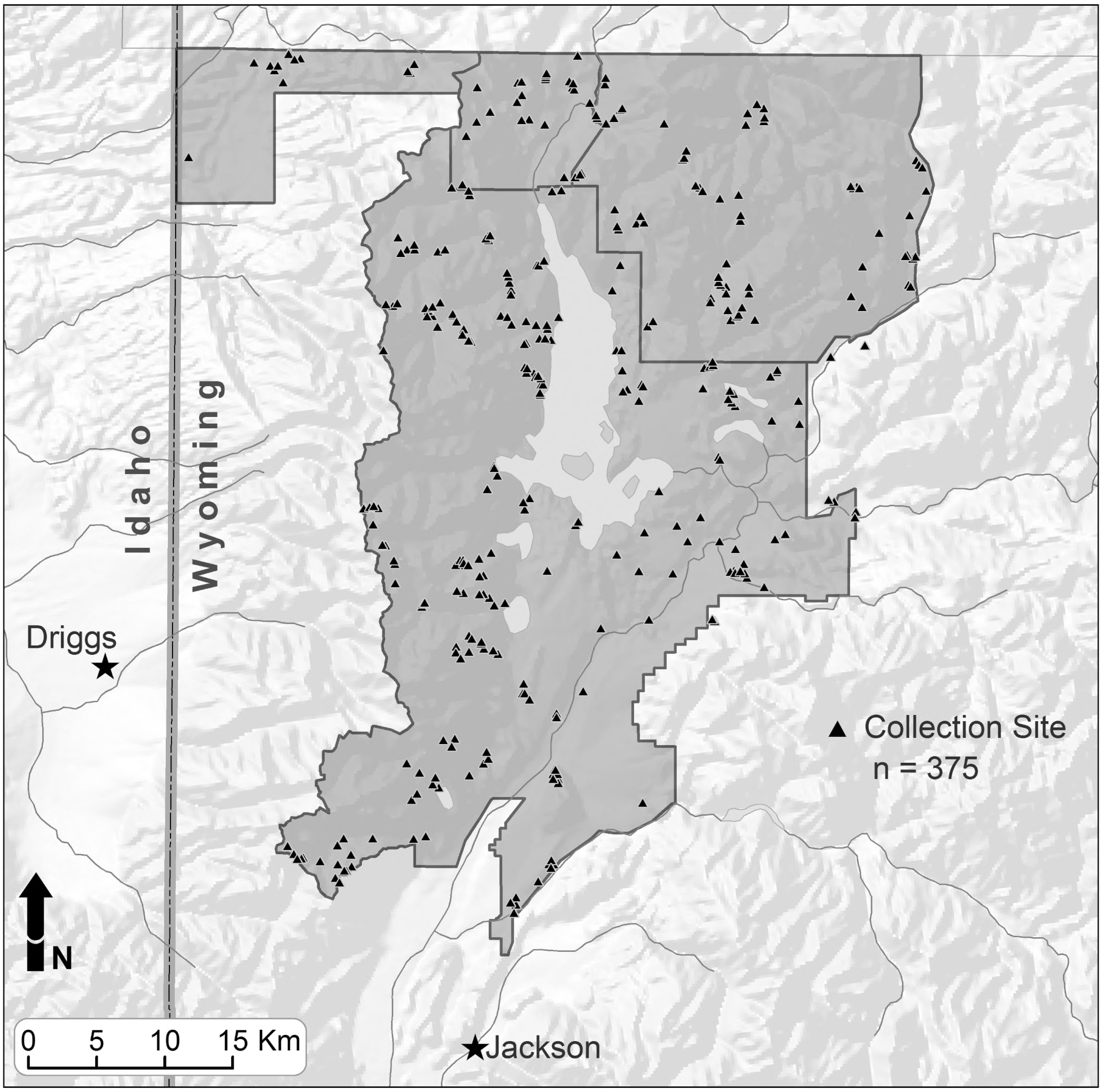

Fig. 2. Localities surveyed in the floristic Inventory of Grand Teton National Park and the Pinyon Peak Highlands, Wyoming. The total number of collecting sites was 375; GPS coordinates were recorded for each.

2003). Correspondingly, erosion striped away the overlying sedimentary layers of Lower Paleozoic age. Third, the largest uplift in the Tetons occurred in recent geologic time (7.5 mya). Movement along the Teton fault, due to extension or pulling, allowed the downthrusting of the Jackson Hole block and an uplift of the Teton block (5 to 1 ratio of drop to lift) (Love et al. 2003). The high and steep east face of the Tetons thus is largely a result of the subsidence of Jackson Hole.

The northern portion of the area has been influenced primarily by the Yellowstone Plateau Volcanic Field. The subterranean plume of superheated magma has led to repeated volcanic activity during the past 2.1 million years (Pierce & Morgan 2009). Furthermore, as the plume is more buoyant, the elevation of the Plateau increased. Two recent volcanic eruptions have shaped the geology. The first was when hot gases and ash poured south into the Highlands, the Parkway, and the Targhee. The resulting tuff (Huckleberry Ridge formation) is widespread across the northern portion of these areas. A later eruption produced the Lewis Canyon Rhyolite, evident in the Parkway (Love et al. 1992).

The Yellowstone Plateau has also influenced the surficial geology by hosting ice masses during the last two glacial periods (Bull Lake and Pinedale). The Plateau's high elevation and cold temperatures produced orographic precipitation that formed large ice sheets. The sheets moved south due to the elevational gradient. The penultimate event, Bull Lake glaciations, (maximum 155,000 years ago) covered most of Jackson Hole and areas to the south (Pierce & Good 1992; Love et al. 2007). Smaller glaciers in the canyons of the Tetons joined this Yellowstone ice mass. It is likely that only the highest elevations in the Tetons and the Highlands were exposed.

The Pinedale glacial maximum (25,000 years ago) also influenced the surficial geology of Jackson Hole (Pierce 2003). The process parallels that of the Bull Lake event but the Yellowstone ice sheet only extended to just south of Jackson Lake. One result was the scouring of the basin now occupied by Jackson Lake (maximum depth 800 feet, 244 m; currently 446 feet, 136 m, deep to sediment level) (Brewer & Thompson 1991; Love et al. 2007).

Many lakes formed on the valley bottom due to scouring (the largest being Emma, Matilda, Two Ocean, Leigh, Jenny). Fine scale effects include numerous pothole ponds (Knight 1994). Finally, when the Yellowstone ice sheet receded, glacial outwash and rivers redistributed large quantities of cobblestone, gravel, and sand.

METHODS

The procedures largely follow practices employed by students and staff at the Rocky Mountain Herbarium for inventories in the region (Hartman 1992; Hartman & Nelson 2008). The main objective is to collect the diversity of vascular plants, in a stratified manner, throughout the growing season. We collected in these four areas during the summers of 2006 (May 27 to Aug 22) and 2007 (June 12 to August 22).

Some specifics on methodology are as follows. When collecting, a route was chosen to sample the greatest diversity of plant habitats. GPS coordinates were taken every 0.5 mile (0.8 km) or less. Often a unique habitat (e.g., bog, neoglacial deposit, alpine communities) was preselected as the destination with frequent collecting in route. About half of the routes were off-trail. The total number of collecting sites was 375 (Figure 2). For rare plants (as designated by the Wyoming Natural Diversity Database, University of Wyoming) (WYNDD), vouchers were taken only for populations that consisted of 20 or more individuals. Specimens were processed at the University of Wyoming/National Park Service Research Station (the AMK Ranch) near Leeks Marina in the Park.

The dried specimens were identified at the RM using appropriate taxonomic literature and then compared with authenticated material. Data for each collection were entered into the RM database (Hartman et al. 2009). The original set of vouchers is housed at the RM and a representative set of duplicates are at the Bridger-Teton National Forest Herbarium in Jackson. The RM vouchers have been mounted and imaged (16.7 megapixels, Canon Mark II). Each high-resolution image is attached to the corresponding entry in the database. They may be viewed from University of Wyoming Digital Iniative website (UWDI 2010) along with the 6,360 images (and database) of specimens housed at the Grand Teton National Park Herbarium (GTNP) (UWDI 2010).

RESULTS AND DISCUSSION

Vegetation Types

Two systems of classification are commonly used to describe plant communities. The first is "community typing" which is based on "existing" vegetation of an area (Cogan et al. 2005). This classification describes assemblages of plants where the dominant species is often used as part of its name. The second system, "habitat typing," describes a community as it would be at "climax." It is a theoretical approach that incorporates succession (Anderson 1986). The following discussion will refer primarily to plant communities of the area – *as they exist today* – yet some comments will cover successional processes as used with habitat typing. This discussion facilitates the listing of relevant vegetation types for each taxon in the Annotated Checklist.

Forests and Woodlands

Subalpine Mixed-Conifer Forest.—Upper treeline is characterized by krummholtz growth forms of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Here, the low-growing common juniper (*Juniperus communis*) may be found. Whitebark pine (*Pinus albicaulis*) is frequent in the subalpine of the Park and in the Highlands where it may be dominant or co-dominant. The *Pinus albicaulis/Vaccinium scoparium* association is most frequent in the Park (Cogan et al. 2005).

The subalpine zone (8,800–9,500 feet; 2,682–2,896 m) is dominated by subalpine fir – Engelmann spruce forests. Seven associations of this type have been described solely for the Park and the Parkway (Cogan et al. 2005), but in most cases this degree of detail will not be addressed. *Acer glabrum* var. *glabrum* and *Ribes montigenum*, are common in the understory of these forests. Named associations include these two shrubs and the following understory species: *Arnica cordifolia*, *Arnica latifolia*, *Luzula glabrata* var. *hitchcockii*, and *Vaccinium scoparium*. A few otherwise conspicuous taxa are *Trisetum spicatum*, *Hedysarum occidentale*, and *Viola purpurea* ssp. *venosa*.

Montane Mixed-Conifer Forest.—These forests are widespread in a zone from 6,400 to 8,900 feet (1,950–2,713 m). Most common is lodgepole pine forest (*Pinus contorta*) with subalpine fir or Engelmann spruce in the understory; thus the broader category, montane mixed conifer. At climax these communities have the last two conifers as dominants; lodgepole pine is nearly always seral (Steele et al. 1983; Habeck 1987).

Shrublands

Montane Shrubland.—Montane slopes are often dominated by shrubs. First is the deciduous shrub community often associated with steep avalanche chutes. Frequent snow slides promote the growth of *Amelanchier* spp., *Sorbus scopulina* var. *scopulina*, *Acer glabrum* var. *glabrum*, *Salix* spp., *Vaccinium* spp., and dwarf individuals of aspen (*Populus tremuloides*). A second is the *Ceanothus velutinus* community that occupies burned areas (Cogan et al. 2005). Associated species are *Symphoricarpos oreophilus* var. *utahensis* and young lodgepole pines. The last shrubland type is usually dominated by *Prunus virginiana* and *Amelanchier* spp. This community type intergrades with Montane Meadow.

Sagebrush Shrubland.—A great deal of interest has centered on the vast expanses of sagebrush shrublands visible across Jackson Hole. Research findings regarding its attributes, in the context of wildlife habitat, are prevalent in the literature (Reed 1952; Martinka 1969; McGee 1982; Chong et al. 2011), yet it has also been described in terms of its floristic elements (Shaw 1958). These areas are easily accessible and thus much-studied. In fact, seventeen associations have been described in the Park and the Parkway where sagebrush species are dominant or codominant (Cogan et al. 2005).

Main shrub components are four species of sagebrush including the most common, *Artemisia tridentata* ssp. *vaseyana*. The other woody taxa are *Purshia tridentata*, *Symphoricarpos oreophilus* var. *utahensis*, and *Linanthus pungens*. The most widespread associations are *Artemisia tridentata* var. *vaseyana–Purshia tridentata/Festuca idahoensis*, *Artemisia tridentata* var. *vaseyana/Hesperostipa comata*, and *Artemisia tridentata* var. *vaseyana/Poa pratensis*.

A rich assemblage of grasses and over a hundred species of forbs can be found in these communities (Reed 1952). Typical grasses are *Achnatherum lettermanii*, *Danthonia intermedia*, *Poa wheeleri*, *Poa pratensis*, and *Pseudoroegneria spicata* ssp. *spicata*. Ubiquitous sedges are *Carex geyeri*, *Carex rossii*, and *Carex hoodii*. Forbs include *Lupinus argenteus* ssp. *rubricaulis*, *Erigeron eatonii* var. *eatonii*, *Astragalus miser* var. *praeteritus*, *Antennaria rosea*, and *Crepis acuminata*.

Willow Bottomland.—Drainages in the lowlands typically are lined by willows while broad canyons with low stream gradients host large areas dominated by willows with occasional stands of blue spruce (*Picea pungens*) or Engelmann spruce. Seasonal flooding may be responsible for adjacent wetlands. Twenty-three associations have been described including distinctive ones with *Salix wolfii* and *Salix geyeriana* (Cogan et al. 2005). Understory diversity is represented by *Angelica arguta*, *Cirsium scariosum*, *Solidago canadensis* var. *salebrosa*, *Betula glandulosa*, *Carex aquatilis* var. *aquatilis*, *Gentianella amarella*, *Mimulus guttatus*, and *Galium trifidum* ssp. *subbiflorum*.

Herblands

Alpine Tundra and Talus.—True alpine conditions promote perennial tufted or mat-forming herbs and ground-hugging shrubs; they are limited to the Park. Topography and aspect dictate the elevation of these communities but most occur above 9,500 feet (2,896 m) (Spence & Shaw 1981). Unique are dwarf shrublands dominated by *Salix arctica*, just above treeline (Cogan et al. 2005). Here and elsewhere are mosaics of meadows, barren areas, patterned ground formed by cryogenic perturbation of soils, rock outcrop, and talus with significant areas consisting of shear rock.

Common mat-formers on the driest microsites include *Phlox multiflora*, *Minuartia obtusiloba*, and *Sibbaldia procumbens*. Representative graminoids include *Agrostis scabra*, *Juncus parryii*, *Carex paysonis*, and *Poa alpina*; also *Deschampsia cespitosa* on mesic sites. Species often associated with cliffs, rock crevices, and talus include *Saxifraga bronchialis* ssp. *austromontana*, *Smelowskia calycina* var. *americana*, *Cryptogramma acrostichoides*, and *Telesonix heucheriformis*.

Subalpine Meadow and Talus.—Meadows adjacent to the subalpine forests vary greatly in size. About half of this zone is characterized by these meadows. They may be lush with tall forb assemblages dominated by *Symphyotrichum ascendens* or *Erigeron peregrinus* ssp. *callianthemus* with a minimal cover of grasses.

The herbaceous perennials *Castilleja sulphurea*, *Epilobium anagallidifolium*, and *Phleum alpinum* are common. Talus slopes and rocky outcrops including cliffs provide habitat for *Leucopoa kingii*, *Erysimum capitatum* var. *capitatum*, and *Penstemon whippleanus*. Mesic sites or stream sides are often inhabited by *Carex microptera*, *Kalmia microphylla*, *Mertensia ciliata*, and *Dodecatheon pulchellum* ssp. *pulchellum*.

Sparsely Vegetated Montane or Subalpine Slope.—Hillsides with the Sparsely Vegetated Montane communities cover extensive areas of the Highlands. They may intergrade with xeric montane grasslands (Cogan et al. 2005) or with limber pine communities (*Pinus flexilis*) that often include Douglas-fir (*Pseudotsuga menziesii*). Rockslides and talus may be placed under the Subalpine Slope type. Frequent associates on open slopes are *Mahonia repens*, *Lomatium ambiguum*, *Crepis* spp., *Phacelia hastata* var. *hastata*, and *Penstemon cyaneus*.

Montane Meadow.—A xeric montane meadow community occurs in the Pinyon Peak Highlands (Cogan et al. 2005). Dry conditions are promoted by well-drained soils or southern exposures; grasses are dominant. More common are the moister meadows with abundant forb cover. Elevations range from 6,500 feet (1,981 m) in the vicinity of Jackson Hole to about 8,800 feet (2,682 m) where they transition to subalpine meadow. Frequent forbs are *Balsamhoriza sagittata*, *Linum lewisii* var. *lewisii*, *Hieracium albiflorum*, *Achillea millefolium* var. *occidentalis*, and *Taraxacum* spp., whereas graminoids include *Melica spectabilis*, *Poa secunda*, *Poa pratensis*, *Carex hoodii*, and *Bromus carinatus*.

Mesic Montane Meadow.—These diverse communities occur at montane elevations but with wet conditions throughout the growing season. Intergradation into stream and seep communities is frequent and some are influenced by thermal springs in the Parkway. Associations listed for the Park and the Parkway are *Mertensia ciliata*, *Heracleum maximum–Rudbeckia occidentalis*, *Geranium viscosissimum*, and *Ligusticum filicinum–Delphinium* ×*occidentale* type which intergrade into subalpine meadows (Cogan et al. 2005). Recurring species include *Gentianopsis thermalis*, *Deschampsia cespitosa*, *Senecio integerrimus* var. *exaltatus*, *Perideridia gairdneri* ssp. *borealis*, and *Calamagrostis canadensis*.

Montane Grassland.—They occur in areas on or near Jackson Hole and are frequently adjacent to sagebrush shrublands. Pastures or old fields also may be of this type. Burned sagebrush communities, not classified under "burned area," usually fall into this category. Representatives include *Koeleria macrantha*, *Poa pratensis*, *Bromus inermis* ssp. *inermis*, and *Antennaria rosea*.

Hydrologically-Influenced Vegetation

Aquatic.—The majority of aquatic habitats are ponds, lakes, and fens occurring below the alpine. Unique aquatic habitats include thermal pools and streams. Free-floating aquatics include *Lemna* spp., while common rooted taxa with floating leaves include *Nuphar lutea* ssp. *polysepala*, *Sagittaria cuneata,* and *Potamogeton* spp. Largely submerged species, often overlooked, include *Isoëtes bolanderi* and *Utricularia macrorhiza*.

Scoured Streambed.—Floristically diverse areas heavily influenced by flood runoff are described below

(Reed 1952). They typically occur where streambeds have a low gradient, such as in the Highlands, northern portions of the Park, and the Parkway. Deposits of sand, gravel, and cobble are often in ribbon mosaics and are typically wet or moist. Sedges and rushes are common, as are species adapted to disturbed areas. Frequently, plants of higher elevations shed propagules that are washed downstream to low elevations, thus appearing as oddities. Woody species may include *Picea pungens* and *Populus angustifolia;* herbs may consist of *Epilobium* spp., *Platanthera* spp., *Heterotheca villosa* var. *depressa*, *Juncus saximontanus*, *Trifolium* spp., *Potentilla arguta*, and *Crepis tectorum*. A local endemic, *Stephanomeria fluminea*, is limited to these habitats.

Stream and Seep.—Perennial and ephemeral riparian habitats and springs are here included. Intergradation with mesic montane meadow, subalpine meadow, scoured streambed, aquatic habitats, willow bottomland, and even montane mixed-conifer forest are possible and may form mosaics. Thus, these communities are diverse and may support *Equisetum arvense*, *Equisetum laevigatum,* and *Botrychium multifidum*. Flowering plants include *Mertensia ciliata*, *Lonicera involucrata, Saxifraga odontoloma*, *Epilobium* spp., *Senecio triangularis,* and *Mentha arvensis,* and a few species of slight stature: *Stellaria longipes* ssp. *longipes*, *Parnassia fimbriata* var. *fimbriata*, and *Spiranthes romanzoffiana*.

Wetland.—Next are habitats that support emergent aquatics. Other communities intergrade: aquatics on the hydric side; montane mesic meadow, stream and seep, and willow bottomland on the drier flanks. Sedges are important and pure stands of *Carex utriculata* or *Carex vesicaria* are common. Likewise, *Poa palustris*, *Agrostis scabra*, *Calamagrostis stricta*, and *Glyceria* spp. provide high canopy cover. Willows are expected, but are a minor component. Herbs include *Eleocharis palustris*, *Carex aurea*, *Juncus ensifolius*, and *Menyanthes trifoliata* as well as *Sium suave* and *Sparganium angustifolium*. Ephemeral ponds may become mud flats and thus classed as "disturbed area."

Disturbed

Aspen Seral Forest.—Aspen forests are promoted by fire yet not classified under "burn areas" due to their successional nature (White et al. 1998). Most are seral, thus the "habitat type" would indicate a climax dominated by conifer (Youngblood 1979). These forest types are rich in herbs, diverse, and physiognomically complex. Sixteen named associations occur in the Park and the Parkway (Cogan et al. 2005).

Burned Area.—The greater extent of these fires occurred in 1988 when nearly half of Yellowstone National Park burned (Christensen et al. 1989). Such areas may be covered by lodgepole pine (Kashian et al. 2004) whereas those previously occupied by shrublands revert to a seral grass community. Exotic species may be frequent, especially near roads and trails. Common species are *Chamerion angustifolium* ssp. *circumvagum*, *Calamagrostis* spp., *Phlox longifolia* ssp. *longifolia*, and *Viola adunca*. Resprouting shrubs such as *Symphoricarpos oreophilus* var. *utahensis* and *Prunus virginiana* var. *melanocarpa* are typical while such communities may also have the fire-obligate *Ceanothus velutinus*.

Roadside-agricultural.—Human-disturbed sites include gravel quarry, parking lot, roadside, homestead, and heavily-used trail. Both non-native and native weeds are conspicuous and may include *Taraxacum laevigatum*, *Carduus nutans*, *Cirsium arvense*, *Tragopogon dubius*, *Capsella bursa-pastoris*, *Medicago lupulina*, *Plantago major*, *Bromus tectorum*, and *Potentilla norvegica*.

TAXON NEWLY DOCUMENTED IN WYOMING

Surprisingly, only one "state record" was documented, an ornamental established in numerous states in the country (2010). *Achillea ptarmica* (*Scott 5641*) is a double-variant cultivar, bred for its showy white ray florets and sold as an ornamental (Thornton-Wood 2000). It was collected near a historic ranch that has seen significant activity for many decades (Daugherty et al. 1999). Irrigation ditches appear to be the corridor for migration.

TAXA NEWLY DOCUMENTED IN THE PARK AND PARKWAY

A comparison was made between Shaw's (1992) "Annotated Checklist of the Vascular Plants of Grand Teton National Park and Teton County, Wyoming" and the results of the inventory of the Park and Parkway. A

total of 112 unique taxa new to these federal lands were obtained in our inventory. Of these, 65 were new to this area based solely on our inventory. An additional 47 unique taxa were also added based on our collections although these had been documented previously based on vouchers in the Grand Teton National Park Herbarium (UWDI 2010) and the Rocky Mountain Herbarium (Hartman et al. 2009).

SPECIES OF SPECIAL CONCERN

Species of conservation concern in Wyoming are designated by the Wyoming Natural Diversity Database (Heidel 2007). Only "Plant Species of Concern," the category covering the rarest plants at the state level (S1, SH) are discussed. They represent 21 species documented at 39 sites. The 21 "Species of Concern," (S2) are so indicated in the checklist. No taxon listed under the Endangered Species Act was encountered nor are any known from northwestern Wyoming.

Achnatherum nevadense (Nevada needlegrass) was collected in a 21 year old burn area with lodgepole pine in the Pinyon Peak Highlands. All other Wyoming localities are east of the Continental Divide in Carbon and Fremont counties. Voucher: *Hartman 82299*.

Agrostis oregonensis (Oregon bentgrass) was collected in the Pinyon Peak Highlands on the margin of a pond with scattered individuals of Engelmann spruce. The WYNDD list indicates uncertainity (S1?) as to its status. Voucher: *Scott 3299*.

Aquilegia formosa (crimson columbine) has a distribution centered in the Pacific Northwest (2010). Its status in Wyoming was previously unknown as the first specimen, collected in 1951, is thought to be a hybrid between *Aquilegia formosa* and *A. flavescens* (Fertig 2000). Voucher: *Scott 961*.

Aspidotis densa (pod-fern) is known from cliff habitats (Shaw 1992). It was collected at montane elevations in the Park. Vouchers: *Nelson 68545*, *68589*.

Astragalus terminalis (railhead milkvetch) is a regional endemic of northwest Wyoming, central Idaho, and southwest Montana that grows on steep, often eroded, and bare slopes (Shaw 1992). It was collected in the Park and the Highlands, all in Jackson Hole. Vouchers: *Hartman 82399*; *Nelson 68354*, *68503*.

Botrychium minganense (Mingan moonwort) is known in Wyoming primarily from sites east of the Continental Divide. It is widespread across the western United States, yet populations probably go unnoticed due to its cryptic form. It was collected in willow bottomlands in the Park. Voucher: *Scott 5690*.

Carex echinata ssp. echinata (little prickly sedge) was collected in all juristictions surveyed. It was obtained in montane wetland and montane mesic meadow. Vouchers: *Scott 1868*, *2283*; *Hartman 86597*, *86612*, *86685*.

Carex proposita (Smoky Mountain sedge) has not been documented in Wyoming since 1899 and thus had been classified as a "historical species" based in the WYNDD list (Fertig 2001; Heidel 2007). The collection was obtained from a subalpine wet meadow in the Park. Voucher: *Scott 1525*.

Cicuta bulbifera (bulb-bearing water-hemlock) was collected in the Targhee on the margin of Tillery Lake. Voucher: *Hartman 86575*.

Gentianopsis simplex (hiker's gentian) was previously known in the state only from Yellowstone (Heidel 2007). The new collections expand its range southward into the Parkway and the Highlands. This species was found in wetlands at the margins of both a thermal and cold springs and a pond with scattered individuals of Engelmann spruce. Vouchers: *Scott 2456*, *3295a*.

Huperzia haleakalae (fir clubmoss) was documented in Wyoming only from a 1932 collection by L. O. Williams. The historical collection and the new record are from the north exposures of the Cathedral Group in the Park. The habitat was a cool, moist, shady cliff ledge in the subalpine. Voucher: *Scott 2666*.

Kelloggia galioides (milk kelloggia) is rare in western Wyoming. It was collected on talus in the montane in the Park. Voucher: *Scott 1889*.

Luzula glabrata var. **hitchcockii** (smooth wood-rush) is locally abundant in the Park (Cogan et al. 2005). It is now recognized as *Luzula hitchcockii* by Swab (2000) as the typical *L. glabrata* is European in distribution. The collections were from the montane to the alpine. Vouchers: *Scott 850*, *3218*, *5260*; *Hartman 82255*.

Minuartia macrantha (House's Stitchwort) was previously recognized as *Minuartia filiorum*, now a synonym of *Minuartia macrantha* (Hartman & Rabeler 2008). It was collected on high elevation limestone in the Park. Voucher: *Scott 5711a*.

Myriophyllum verticillatum (whorled water-milfoil) is an aquatic documented once in the Park. Previously it was known in Wyoming only from Yellowstone National Park and the Shoshone National Forest (Heidel 2007). Voucher: *Scott 2543*.

Porterella carnosula (western porterella) is a showy annual, locally abundant in drying ponds. It was collected in the Park. Voucher: *Scott 5421*.

Scheuchzeria palustris (pod-grass) is known from bogs in Yellowstone (Lemly 2007). The population in Targhee extends its Wyoming range a bit to the south. Voucher: *Hartman 86799*.

Spirodela polyrhiza (duckmeat) was collected in the Highlands and in northeastern portions of the Park. Most small populations do not overwinter, but must be established anew or at other sites through introductions on the feet of waterfowl. Thus they are difficult to track over time (Landolt 2000). Vouchers: *Scott 2380*, *3818*, *4098*, *4412*.

Stellaria crispa (crimped stitchwort) is known from mesic habitats of northwest Wyoming. Thus its occurrence in this Park is limited. Vouchers: *Scott 990*, *1954*; *Hartman 86755*.

Viola renifolia (kidney leaf white violet) is new to the Park where it was collected in a willow bog. Voucher: *Nelson 68832*.

Xerophyllum tenax (western beargrass) is abundant just south of Yellowstone where it was documented in the Park, the Parkway, and the Targhee. Vouchers: *Scott 2977*, *3990*, *5436*.

INVASIVE PLANTS

Invasive plants of exotic origins pose certain threats to ecosystems and human economies. Because these threats can be insidious and persistent, noxious weeds are carefully monitored by governmental agencies. In Wyoming, the state legislation has designated 25 plant species as "noxious" (Wyoming Weed and Pest Council 2008). This study identified nine such taxa; nearly all were collected in human-disturbed areas (see The Annotated Checklist). Exceptions were three species obtained from areas seemingly free from such disturbance: *Cirsium arvense*, *Linaria vulgaris*, and *Sonchus arvensis*. The first two were found in the backcountry at multiple sites.

Teton County has established a list of "Declared Weeds" that compliments the state list of noxious plants (Wyoming Weed and Pest Council 2007). The three species, collected along roads or developed sites, are *Berteroa incana*, *Cirsium vulgare*, and *Verbascum thapsus*.

Roughly 7.5 percent (72 species) of the documented taxa are not native to North America (USDA 2010). This is a relatively low number as levels of 12 to 14 percent have been typical in other studies through the RM (Hartman et al. 2009).

SUMMARY OF TAXA

A summary of collection results for the study follows. Numbers in parentheses are the subset for the Park and Parkway.

List by taxonomic category			List by special category		
Families	86	(82)	Exotic taxa	72	(69)
Genera	347	(338)	Percent exotic taxa	7.5	(7.6)
Species	904	(861)	WY Noxious weeds	9	(8)
Infraspecies	52	(42)	Species conservation concern	42	(37)
Hybrids	6	(6)	State records	1	(1)
Unique taxa	962	(909)	Taxa new to the Park and Parkway		(112):
			this study		(65)
			this and other studies		(47)

List of unique taxa by major plant group.

Fern Allies	10	(10)
Ferns	12	(12)
Gymnosperms	9	(9)
Angiosperms	931	(878)
Total	**962**	**(909)**

CONCLUSIONS

The entire summers of 2006 and 2007 were devoted to inventorying the vascular plants of Grand Teton National Park, the J. D. Rockefeller Jr. Memorial Parkway, a portion of the Targhee National Forest, and the Pinyon Peak Highlands, Bridger-Teton National Forest. Detailed collecting was done at 375 sites (Fig. 2).

A total of 962 unique taxa (904 species, 52 infraspecies) in 347 genera and 86 families were documented in the study. Also, six hybrid taxa, as documented in the literature, were collected. For the Park and Parkway proper, the relevant numbers are 909 unique taxa (861 species, 42 infraspecies, and 6 hybrids).

The following botanists obtained a total of 8,002 numbered voucher specimens: David Scott, 5,752 collections, Ronald L. Hartman, 1,351, and B.E. Nelson, 899.

We documented one Wyoming record, the cultivar *Achillea ptarmica*, one local endemic, *Stephanomeria fluminea* described 12 years ago (Gottlieb 1999), and a number of regional endemics. Species of conservation totaled 42 vouchered at 89 sites. Finally, 112 unique taxa new to the Park and Parkway have been documented.

Roughly 7.5 percent (72 species) of the flora is not native to North America. Of these exotics, nine species are considered "Noxious" in Wyoming.

THE ANNOTATED CHECKLIST

The checklist is divided into major vascular plant groups (ferns and fern allies, gymnosperms, and angiosperms) each with alphabetical listings by family and species. Nomenclature follows PLANTS database (USDA 2010). In cases where names differ from those in Dorn's Vascular Plants of Wyoming (2001), the latter name is placed in brackets.

Following is a guide to format and abbreviations associated with individual taxa in the checklist. Collection data are available online (Hartman et al. 2009).

Taxon with Authority **Federal entities [G,W,H,T]** elevational range in feet; GEOLOGIC AREA **[number of collections]** vegetation type.

[*Synonym* with Authority] based on Dorn (2001). If the binomial for the synonym is the same for the accepted name, the authority is omitted]

Entity abbreviations:

G **G**rand Teton National Park
W J.D. Rockefeller Jr. Memorial Park **W**ay
H Pinyon **H**ighlands, Bridger-Teton National Forest
T **T**arghee National Forest

Geologic area:

JAC Jackson Hole
PPH Pinyon Peak Highlands
TET Teton Mountains
YEL Yellowstone Plateau (J. D. Rockefeller Jr. Memorial Parkway and Targhee National Forest)

Habitat type:

alt Alpine tundra
aqu Aquatic
asf Aspen seral forest
bua Burned area
clf Cliffside or cliff ledge
mos Montane shrubland
sas Sagebrush shrubland
sum Subalpine meadow
scs Scoured streambed
smc Subalpine mixed-conifer forest

dis	Disturbed area	**sps**	Sparsely vegetated montane or subalp. slope
mm	Montane meadow	**str**	Stream and seep
mmm	Montane mesic meadow	**tas**	Talus and scree
mmc	Montane mixed-conifer forest	**wet**	Wetland
mog	Montane grassland	**wib**	Willow bottomland

Symbols by category preceeding Taxon

●	Exotic to North America
▲	"Noxious," weeds so designation in Wyoming
►	Taxon new to Park and Parkway, this study
◄	Taxon new to Park and Parkway, this study and other collections
>	Plant Species of [Conservation] Concern (S1, SH) (WYNDD; Heidel 2007)
<	Species of [Conservation] Concern (S2) (WYNDD; Heidel 2007)
×	Hybrid

FERN ALLIES

Equisetaceae

Equisetum arvense L. **[G,W,H,T]** 6527–8885'; JAC, PPH, TET, YEL **[23]** mmm, scs, str, wet, wib.

Equisetum hyemale L. var. *affine* (Engelm.) A.A. Eat. **[G,H,T]** 6527–7000'; JAC, YEL **[4]** mmm, mmc, sps, wet.

Equisetum laevigatum A. Br. **[G,W,H]** 6551–7200'; JAC, PPH, YEL **[11]** sas, scs, str, wet, wib.

Equisetum variegatum Schleich. ex Weber & Mohr var. *variegatum* **[G,H]** 6860–7780'; JAC, PPH **[8]** scs, str, wet. [*Equisetum variegatum*]

Isoetaceae

Isoëtes bolanderi Engelm. **[G,T]** 7340–9530'; TET, YEL **[2]** aqu.

Lycopodiaceae

> *Huperzia haleakalae* (Brack.) Holub **[G]** 9520'; TET **[1]** alt, clf.

Lycopodium annotinum L. **[G]** 7825'; TET **[1]** mmc, str.

Ophioglossaceae

► > *Botrychium minganense* Vict. **[G]** 7350'; TET **[1]** wib.

Botrychium multifidum (S.G. Gmel.) Trevisan **[G,W,H,T]** 6333–7539'; JAC, PPH, YEL **[10]** mmm, mmc, str, wet.

Selaginellaceae

Selaginella densa Rydb. **[G,H]** 6700–10800'; JAC, TET **[14]** alt, clf, sas, sps, str, tas.

FERNS

Aspleniaceae

< *Asplenium trichomanes-ramosum* L. **[G]** 9320–9635'; TET **[3]** clf.

Dennstaedtiaceae

Pteridium aquilinum (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller **[G]** 6800–7200'; TET **[1]** mos.

Dryopteridaceae

< *Athyrium americanum* (Butters) Maxon. **[G]** 9590–10160'; TET **[2]** tas. [*Athyrium distentifolium* Tausch ex Opiz. var. *americanum* (Butters) Cronq.]

Athyrium filix-femina (L.) Roth **[G]** 6868'; JAC **[1]** str.

Cystopteris fragilis (L.) Bernh. **[G,W]** 7000–10060'; TET, YEL **[27]** alt, clf, mos, sps, sum, tas.

► *Dryopteris filix-mas* (L.) Schott **[G]** 6800–7200'; TET **[1]** mos.

< *Gymnocarpium disjunctum* (Rupr.) Ching **[G]** 6824'; TET **[1]** str.

Polystichum lonchitis (L.) Roth **[G]** 8285–9400'; TET **[4]** clf, mmc, smc, tas.

Woodsia scopulina D.C. Eat. **[G]** 7200–9200'; TET **[3]** sps, tas.

Pteridaceae

> *Aspidotis densa* (Brack.) Lellinger **[G]** 7200–8000'; TET **[2]** clf, sps.

Cryptogramma acrostichoides R. Br. **[G]** 7000–10800'; TET **[17]** alt, clf, mmc, mos, sps, tas.

Pellaea breweri D.C. Eat. **[G,H]** 6938'; JAC, TET **[6]** alt, clf, sum, sps, tas.

GYMNOSPERMS

Cupressaceae

Juniperus communis L. var. *depressa* Pursh **[G,H]** 6640–10000'; JAC, PPH, TET **[16]** asf, clf, sps, mmc, tas.

Juniperus scopulorum Sarg. **[G,H]** 6860–7367'; JAC, TET **[4]** asf, bua, clf, sps.

Pinaceae

Abies lasiocarpa (Hook.) Nutt. var. *lasiocarpa* **[G,W,H]** 6700–9485'; JAC, PPH, TET, YEL **[20]** bua, mmc, mos, smc.

Picea engelmannii Parry ex Engelm. **[G,H]** 6920–9800'; JAC, PPH, TET **[16]** mmc, scs, smc, sps.

Picea pungens Engelm. **[G,H]** 6640–6865'; JAC **[5]** asf, scs, wet, wib.

Pinus albicaulis Engelm. **[G,H]** 6758–9620'; JAC, PPH, TET **[7]** sum, smc, sps.

Pinus contorta Dougl. ex Loud. var. *latifolia* Engelm. ex Wats. **[G,H,T]** 6700–8360'; JAC, PPH, TET, YEL **[33]** asf, bua, mmc, sas.

Pinus flexilis James **[G]** 6700–7367'; JAC **[3]** mmc, sps.

Pseudotsuga menziesii (Mirb.) Franco var. *glauca* (Beissn.) Franco **[G,H]** 6700–9200'; JAC, TET **[20]** asf, bua, mmc, sas, sps, str, tas.

ANGIOSPERMS

Aceraceae

Acer glabrum Torr. var. *glabrum* **[G,H]** 6824–9300′; JAC, PPH, TET **[12]** clf, mmc, mos, smc, sps, tas.

Alismataceae

Sagittaria cuneata Sheld. **[G,W,H]** 6845–7549′; JAC, PPH, YEL **[6]** aqu, wet.

Apiaceae

Angelica arguta Nutt. **[G,W,H,T]** 6460–10250′; JAC, PPH, TET, YEL **[10]** mmm, mmc, str, wet, wib.

Angelica pinnata Wats. **[G,W,H]** 6820–8360′; JAC, PPH, TET, YEL **[13]** mmm, mmc, scs, str, wet, wib.

Angelica roseana L. F. Hend. **[G,H]** 7785–10040′; TET **[3]** alt, smc, tas.

Bupleurum americanum Coult. & Rose **[G]** 9607–10875′; TET **[4]** alt, clf, sps, tas.

> *Cicuta bulbifera* L. **[T]** 7340′; YEL **[1]** str.

Cicuta maculata L. var. *angustifolia* Hook. **[W,T]** 6527–6859′; YEL **[3]** str, wet.

Heracleum maximum Bartram **[G,W,H]** 6816–8885′; JAC, PPH, TET, YEL **[14]** mmm, mmc, str, wet. [*Heracleum sphondylium* L. var. *lanatum* (Michx.) Dorn]

Ligusticum canbyi (Coult. & Rose) Coult. & Rose **[W,H,T]** 6880–8320′; PPH, YEL **[4]** mmm, mmc, str.

Ligusticum filicinum Wats. **[G,W,H,T]** 6920–10100′; JAC, PPH, TET, YEL **[19]** bua, mmc, sum, str, sps.

Lomatium ambiguum (Nutt.) Coult. & Rose **[G,H]** 6551–8320′; JAC, PPH, TET **[25]** bua, mmc, scs, sps.

Lomatium cous (Wats.) Coult. & Rose **[G,W]** 6397–9640′; JAC, PPH, TET, YEL **[10]** sas, smc, sps, wet.

Lomatium dissectum (Nutt.) Math. & Const. var. *multifidum* (Nutt.) Math. & Const. **[G,H]** 6800–8400′; PPH, TET **[7]** mos.

Lomatium simplex (Nutt.) Macbr. var. *simplex* **[G,W,H]** 6397–9200′; JAC, PPH, TET, YEL **[27]** asf, bua, dis, mmc, mos, sas. [*Lomatium triternatum* (Pursh) Coult. & Rose var. *platycarpum* (Torrey) Boivin]

Orogenia linearifolia Wats. **[G,W,H]** 6520–8640′; JAC, PPH, TET, YEL **[4]** mm, dis, sas.

Osmorhiza berteroi DC. **[G,W,H,T]** 6700–7760′; JAC, PPH, TET, YEL **[11]** mm, mmc, sas, str.

Osmorhiza depauperata Phil. **[G,H]** 6760–6938′; JAC, PPH, TET **[13]** mm, mmc, mos, sps, str.

Osmorhiza occidentalis (Nutt. ex T. & G.) Torr. **[G,H]** 6520–8500′; JAC, PPH, TET **[8]** mos, sas, sps, wib.

Perideridia bolanderi (A. Gray) Nels. & Macbr. ssp. *bolanderi* **[G]** 6520–6938′; JAC **[4]** mm, mmc, sps.

Perideridia gairdneri (Hook. & Arn.) ssp. *borealis* T.I. Chuang & Constance **[G,W,H]** 6780–8320′; JAC, PPH, TET, YEL **[19]** mm, mmm, mmc, mog, sps, wet, wib. [*Perideridia montana* (Blank.) Dorn]

Pteryxia hendersonii (Coult. & Rose) Mathias & Constance **[G,H]** 9300–10795′; TET **[16]** alt, clf, sps, tas. [*Cymopterus longilobus* (Rydb.) W. A. Weber]

Pteryxia terebinthina (Hook.) Coult. & Rose var. *albiflora* (T. & G.) Mathias **[G]** 6980–7080′; JAC **[1]** sps. [*Cymopterus terebinthinus* (Hook.) T. & G. var. *albiflorus* (T. & G.) Jones]

► < *Sanicula graveolens* Poepp. ex DC. **[G,H]** 7800–9200′; JAC, PPH, TET **[4]** mm, sps.

Sium suave Walt. **[G,H,T]** 6400–7550′; JAC, PPH, YEL **[4]** mmm, wet, wib.

► *Zizia aptera* (A. Gray) Fern. **[G]** 6400–6790′; JAC **[3]** wet, wib.

Apocynaceae

Apocynum androsaemifolium L. **[G,W,H]** 6932–8130′; JAC, PPH, TET, YEL **[6]** mmc, mm, sps.

►× *Apocynum* ×*floribundum* Greene **[G]** 6823–8400′; JAC, TET **[3]** mm, mos, sum.

Asteraceae

Achillea millefolium L. var. *occidentalis* DC. **[G,W,H,T]** 6333–10450′; JAC, PPH, TET, YEL **[49]** alt, bua, mm, mmm, mmc, mog, mos, sum, scs, sps, tas, wet, wib. [*Achillea millefolium* var. *lanulosa* (Nutt.) Piper]

● *Achillea ptarmica* L. **[G]** 6760–6740′; JAC **[1]** dis.

Agoseris aurantiaca (Hook.) Greene **[G,W,H]** 6824–10060′; JAC, PPH, TET, YEL **[20]** alt, bua, mm, mmc, mos, sps, wib.

Agoseris glauca (Pursh) Raf. var. *glauca* **[G,H]** 6780–9680′; JAC, PPH, TET **[11]** mmm, sum, sps, str, wib.

Agoseris glauca (Pursh) Raf. var. *dasycephala* (T. & G.) Jeps. **[G,W,H,T]** 6527–10600′; JAC, PPH, TET, YEL **[34]** bua, mm, mmc, mos, scs, sps, str, tas, wet, wib.

Agoseris glauca (Pursh) Raf. var. *laciniata* (D.C. Eat.) Smiley **[G,H]** 6560–10350′; JAC, PPH, TET **[10]** alt, bua, sas, tas.

◄ *Agoseris lackschewitzii* D. M. Hend. & Moseley **[G,W,H]** 6900–9780′; JAC, PPH, TET, YEL **[4]** bua, mmm, scs.

Anaphalis margaritacea (L.) Benth. **[G,W,H,T]** 6900–7740′; JAC, PPH, TET, YEL **[25]** mm, mmm, mmc, mos, scs, sps, wet.

Antennaria anaphaloides Rydb. **[G,H]** 7000–8310′; JAC, PPH, TET **[4]** bua, scs, str.

Antennaria aromatica Evert **[G]** 10000′; TET **[1]** tas.

Antennaria corymbosa E. Nels. **[G,W,H]** 6750–8680′; JAC, PPH, YEL **[10]** mm, mmm, mog, wib.

Antennaria dimorpha (Nutt.) T. & G. **[G]** 7367′; JAC **[1]** sps.

Antennaria lanata (Hook.) Greene **[G]** 9665′; TET **[1]** tas.

◄ *Antennaria luzuloides* T. & G. **[G,H]** 6551–8000′; JAC, PPH, TET **[13]** mm, sas, scs.

Antennaria media Greene **[G]** 9240–10795′; TET **[10]** alt, clf, sum, tas.

Antennaria microphylla Rydb. **[G,H]** 6551–10640′; JAC, PPH, TET **[24]** alt, asf, bua, mm, mmc, sps.

Antennaria parvifolia Nutt. **[G]** 6840′; TET **[1]** mm.

◄ *Antennaria pulcherrima* (Hook.) Greene **[G,W,H]** 6790–6820′; JAC, PPH, YEL **[4]** mmc, str, wet.

Antennaria racemosa Hook. **[G, W,H]** 6700–8720′; JAC, PPH, TET, YEL **[18]** bua, mm, mmc, sps, tas.

Antennaria rosea Greene **[G,W,H]** 6700–9740′; JAC, PPH, TET, YEL **[54]** alt, mm, mmm, mmc, mog, sas, scs, sps.

Antennaria umbrinella Rydb. **[G,H]** 7020–11320′; JAC, TET **[16]** alt, sas, tas.

Arnica chamissonis Less. var. *andina* (Nutt.) Ediger &T.M. Barkley **[G,W,H]** 7160–7860′; JAC, PPH, TET, YEL **[6]** mmm, mmc, scs, tas, wib. [*Arnica chamissonis* var. *foliosa* (Nutt.) Maguire]

Arnica cordifolia Hook. **[G,W,H]** 6594–9485′; JAC, PPH, TET, YEL **[44]** bua, mm, mmc, sas, sum, smc, tas.

Arnica latifolia Bong. **[G,H]** 6823–10350′; JAC, PPH, TET **[15]** alt, mm, mmc, mos, sps, tas.

Arnica longifolia D.C. Eat. **[G,W,H]**7230–10800′; PPH, TET, YEL **[11]** alt, sps, str, tas, wib.

Arnica mollis Hook. **[G,H,T]** 6460–10060′; JAC, PPH, TET, YEL **[15]** alt, mm, mmc, scs, str.

Arnica parryi A. Gray var. *parryi* **[G,H,T]** 7120–8360′; PPH, TET, YEL **[7]** mm, mmc, scs.

► *Arnica rydbergii* Greene **[G]** 7210–10800′; TET **[7]** alt, smc, sps, tas.

Arnica sororia Greene **[G]** 6560′; JAC **[1]** bua.

Artemisia arbuscula Nutt. ssp. *arbuscula* **[G]** 6975′; JAC **[1]** mog.

◄ *Artemisia arbuscula* Nutt. ssp. *thermopola* Beetle **[G,W]** 6810–6880′; JAC **[2]** dis, mmc.

Artemisia dracunculus L. **[G,H]** 6935–7790′; JAC, PPH **[4]** mmc, scs, str.

Artemisia ludoviciana Nutt. ssp. *ludoviciana* **[H]** 7740′; PPH **[1]** scs.

Artemisia ludoviciana Nutt. ssp. *candicans* (Rydb.) D.D. Keck **[G,W,H]** 6770–9300′; JAC, PPH, TET **[10]** alt, dis, sum, scs, wib. [*Artemisia ludoviciana* var. *latiloba* Nutt.]

Artemisia scopulorum A. Gray **[G]** 10640′; TET **[1]** alt.

Artemisia tridentata Nutt. ssp. *vaseyana* (Rydb.) Beetle **[G]** 6400–6975′; JAC **[2]** mog.

Artemisia tripartita Rydb. ssp. *tripartita* **[G]** 6400′; JAC **[1]** mm.

Balsamorhiza sagittata (Pursh) Nutt. **[G,H]** 6397–8985′; JAC, PPH, TET, YEL **[43]** mm, mmm, mmc, sas, str.

Bidens cernua L. **[G,T]** 6400–7340′; JAC, YEL **[7]** str, wet.

▲● *Carduus nutans* L. **[G,W]** 6597–6845′; JAC **[5]** dis, scs.

▲● *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek **[G]** 6840′; JAC **[1]** dis. [*Centaurea maculosa* Lam.]

Chaenactis douglasii (Hook.) H. & A. var. *douglasii* **[G,H]** 7367–10350′; JAC, PPH, TET **[5]** sps, tas. [*Chaenactis douglasii* var. *montana* Jones]

Chaenactis douglasii (Hook.) Hook. & Arn. var. *alpina* A. Gray **[G]** 10600′; TET **[1]** alt, tas. [*Chaenactis alpina* (A. Gray) Jones var. *alpina*]

▲● *Cirsium arvense* (L.) Scop. **[G,W,H,T]** 6780–8360′; JAC, PPH, TET, YEL **[9]** bua, dis, mm, mmc, mog, wet, wib.

Cirsium eatonii (A. Gray) Robins. **[G]** 8878–11320′; TET **[8]** alt, sps, tas.

Cirsium scariosum Nutt. **[G,W,H]** 6573–7255′; JAC, PPH, TET, YEL **[9]** mm, mmc, wet, wib.

● *Cirsium vulgare* (Savi) Tenore **[W]** 6810–6840′; YEL **[2]** dis, wet.

Crepis acuminata Nutt. **[G,H]** 6560–7180′; JAC **[9]** asf, bua, mmc, mog, sas, sps.

Crepis atribarba Heller **[G,H]** 6700–7160′ JAC, PPH, TET **[9]** alt, mmc, mog, sas, sps.

◄ *Crepis intermedia* A. Gray **[G,H]** 7040–8130′; JAC, PPH, TET **[6]** mm, mos, sps.

Crepis modocensis Greene ssp. *modocensis* **[G,H]** 6700–7180′; JAC **[2]** sas, sps.

Crepis nana Richards. ssp. *ramosa* Babc. **[H]** 9590′; PPH **[1]** sps.

● *Crepis tectorum* L. **[G,W,H,T]** 6333–7740′; JAC, PPH, TET, YEL **[21]** mm, mmc, mog, sas, scs, wet, wib.

Ericameria suffruticosa (Nutt.) G.L. Nesom **[G]** 8600–10450′; TET **[3]** alt, mmc.

Erigeron acris L. ssp. *debilis* (A. Gray) Piper **[G]** 6824′; TET **[1]** str. [*Erigeron acris* var. *kamtschaticus* (DC.) Herder]

Erigeron concinnus (H. & A.) T. & G. var. *concinnus* **[G,H]** 6560–7160′; JAC **[10]** bua, sas, sps. [*Erigeron pumilus* Nutt. var. *concinnus* (H. & A.) Dorn]

Erigeron compositus Pursh **[G]** 6550–10000′; JAC, TET **[23]** alt, clf, mm, mmc, mog, sas, sps, tas. [*Erigeron compositus* var. *discoideus* A. Gray]

Erigeron corymbosus Nutt. **[G]** 6560–7160′; TET **[4]** bua, sas, sps.

Erigeron divergens T. & G. **[G,W]** 6550–7155′; JAC, YEL **[8]** bua, mos, sas.

Erigeron eatonii A. Gray var. *eatonii* **[G,H]** 6700–8000′; JAC, PPH, TET **[22]** mm, mmc, sas, sum, smc, scs, sps.

Erigeron glabellus Nutt. var. *glabellus* **[G]** 6400–6852′; JAC **[5]** dis, mmc, wet.

Erigeron gracilis Rydb. **[H]** 8320′; PPH **[1]** mmm.

Erigeron leiomerus A. Gray **[G,H]** 8878–11320′; TET **[12]** alt, sps, tas.

Erigeron lonchophyllus Hook. **[G,H]** 7185–7740′; JAC, PPH, TET **[8]** mmm, scs, wet, wib.

Erigeron ochroleucus Nutt. var. *scribneri* (Canby ex Rydb.) Cronq. **[G]** 8975′; TET **[1]** sum.

Erigeron peregrinus (Banks ex Pursh) Greene ssp. *callianthemus* (Greene) Cronq. **[G,H]** 8450–10305′; PPH, TET **[16]** alt, clf, mm, mmc, smc, str, tas. [*Erigeron peregrinus* var. *scaposus* (T. & G.) Cronq.]

Erigeron simplex Greene **[G]** 9520–10305′; TET **[7]** alt, clf, mm, sps.

Erigeron speciosus (Lindl.) DC. **[G,W,H]** 6232–9680′; JAC, PPH, TET, YEL **[15]** mm, mmc, sas, sum.

Erigeron strigosus Muhl. ex Willd. var. *septentrionalis* (Fern. & Wieg.) Fern. **[W]** 6859′; YEL **[1]** wet. [*Erigeron strigosus*]

► *Erigeron tweedyi* Canby **[G]** 7785′; TET **[1]** sps, tas.

Erigeron ursinus D.C. Eat. **[G,H]** 9140–10350′; PPH, TET **[8]** mmc, sum, smc, sps, tas.

Eriophyllum lanatum (Pursh) Forbes var. *integrifolium* (Hook.) Smiley **[G,H]** 6597–9620′; JAC, PPH, TET **[25]** mm, mmc, sas, sum, sps, wib.

Eucephalus elegans Nutt. **[G]** 8000′; TET **[1]** mmc.

Eucephalus engelmannii (D.C. Eaton) Greene **[G,W,H]** 6824–10450′; PPH, TET, YEL **[11]** alt, mmc, sps.

Eurybia glauca (Nutt.) G.L. Nesom **[G]** 8885–8375′; TET **[1]** mm. [*Eucephalus glaucus* Nutt.]

Eurybia integrifolia (Nutt.) G.L. Nesom **[G,W,H,T]** 6527–10450′; JAC, PPH, TET, YEL **[13]** mm, mmc, sum, sps.

Eurybia merita (A. Nelson) G.L. Nesom **[G]** 6795′; JAC **[1]** mmc.

Gnaphalium palustre Nutt. **[G,W,H]** 6680–7980′; JAC, PPH, YEL **[6]** bua, dis, mmm, str, wet.

Helianthella quinquenervis (Hook.) A. Gray **[G,H]** 6995–8420′; JAC, PPH, TET **[7]** mm, mmc.

Helianthella uniflora (Nutt.) T. & G. var. *uniflora* **[G,W,H]** 6932–8915′; JAC, PPH, TET **[17]** mm, mmc, mos, sas.

Heliomeris multiflora (Nutt.) var. *multiflora* **[G,W,H]** 6840–7790′; JAC, PPH, TET, YEL **[4]** mm, mmc, str, wet. [*Viguiera multiflora* (Nutt.) Blake var. *multiflora*]

Heterotheca villosa (Pursh.) Shinners var. *depressa* (Rydb.) Semple **[G,H]** 6760–7740′; JAC, PPH **[4]** scs. [*Heterotheca depressa* (Rydb.) Dorn]

Hieracium albiflorum Hook. **[G,W,H]** 6800–8360′; JAC, PPH, TET, YEL **[20]** bua, mm, mmc, mog, mos, str.
Hieracium cynoglossoides Arv.-Touv. **[G,W,H,T]** 7200–8885′; JAC, PPH, TET, YEL **[7]** bua, mm, mmc.
Hieracium gracile Hook. var. *gracile* **[G,H]** 7210–10350′; PPH, TET **[13]** alt, clf, mm, mmc, sum, tas. [*Hieracium triste* Willd. ex Spreng. var. *gracile (*Hook.) A. Gray]
Hieracium scouleri Hook. var. *scouleri* **[W]** 6920′; PPH **[1]** mmc.
Lactuca tartarica (L.) C. A. Mey. var. *pulchella* (Pursh) Breitung **[H]** 7790′; PPH **[1]** mmc. [*Lactuca oblongifolia* Nutt.]
● *Lactuca serriola* L. **[G,T]** 6515–6845′; **[3]** dis, wet.
▲● *Leucanthemum vulgare* Lam. **[G]** 6680′; JAC **[2]** dis, mmc. [*Chrysanthemum leucanthemum* L.]
►● *Logfia arvensis* (L.) Holub **[G]** 6700′; JAC **[1]** dis.
Machaeranthera canescens (Pursh) A. Gray var. *canescens* **[G]** 8400′; TET **[1]** clf, sum. [*Machaeranthera canescens* var. *monticola* Dorn]
Madia glomerata Hook. **[G,W,H]** 6840–8310′; JAC, PPH, TET, YEL **[7]** dis, mm, mog, wet.
● *Matricaria discoidea* DC. **[G]** 6760–6820′; JAC **[2]** dis, sas, wib. [*Matricaria matricarioides* (Less.) Porter]
Microseris nutans (Hook.) Schultz-Bip. **[G,H]** 6520–8160′; JAC, PPH, TET **[29]** mm, mmc, mos, sas, sps, str.
► *Nothocalais nigrescens* (L. F. Hend.) Heller **[W,H]** 6900–8270′; PPH, YEL **[2]** mm, str.
Oreostemma alpigenum (Torr. & A. Gray) Greene var. *haydenii* (Porter) G.L. Nesom **[G]** 9590–10795′; YEL **[10]** alt, clf, sum, sps.
Packera cana (Hook.) W. A. Weber & A. Löve **[G]** 7600–10795′; TET **[8]** alt, clf, mog, sps.
Packera dimorphophylla (Greene) W. A. Weber & A. Löve var. *paysonii* (T. M. Barkl.) T. M. Barkl. & Trock **[G]** 7860–10000′; TET **[8]** alt, mm, sum, sps.
Packera multilobata (T. & G. ex A. Gray) Weber & A. Löve **[G]** 7390′; PPH **[1]** str.
Packera paupercula (Michx.) A. Löve & D. Löve **[G]** 6790–6850′; JAC **[2]** mmm, str.
► *Packera pseudaurea* (Rydb.) W. A. Weber & A. Löve var. *pseudaurea* **[G,W,H,T]** 6460–7300′; JAC, PPH, TET, YEL **[7]** mmm, mmc, str, wet, wib.
Packera streptanthifolia (Greene) W. A. Weber & A. Löve **[G,H]** 6400–10795′; JAC, PPH, TET, YEL **[52]** alt, asf, mm, mmc, mog, mos, sas, scs, sps, str, tas.
► *Packera subnuda* (DC.) Trock & T. M. Barkl. **[W]** 7155′; YEL **[1]** wet.
Packera werneriifolia (A. Gray) W. A. Weber & A. Löve **[G]** 10295′; TET **[1]** alt, sps.
Pseudognaphalium macounii (Greene) Kartesz **[G,W,H,T]** 6527–7549′; PPH, TET, YEL **[4]** bua, dis, mmc, sps. [*Gnaphalium viscosum* H.B.K.]
Rudbeckia occidentalis Nutt. **[G,W,H,T]** 6460–8320′; JAC, PPH, TET, YEL **[22]** mm, mmm, mmc, scs, wib.
Senecio amplectens A. Gray var. *holmii* (Greene) Harrington **[G]** 10171′; TET **[1]** sps. [*Ligularia amplectens* (A. Gray) Weber var. *holmii* (Greene) Dorn]
Senecio crassulus A. Gray **[G,W,H]** 6960–10600′; JAC, PPH, TET, YEL **[17]** alt, mm, mmm, mmc, sum, smc, str.
Senecio fremontii T. & G. var. *fremontii* **[G]** 8878–10305′; TET **[12]** alt, sps, tas.
Senecio hydrophilus Nutt. **[G,W,T]** 6460–7160′; JAC, YEL **[7]** str, wet.
Senecio integerrimus Nutt. var. *exaltatus* (Nutt.) Cronq. **[G,W,H]** 6400–8400′; JAC, PPH, TET, YEL **[28]** mm, mmm, mmc, mog, mos, sas, sum.
Senecio serra Hook. var. *serra* **[G]** 6935–7200′; JAC **[2]** mmc, str.
Senecio triangularis Hook. **[G,W,H]** 6800–10640′; JAC, PPH, TET, YEL **[19]** alt, clf, mmm, mmc, sas, str, wet.
Solidago canadensis L. var. *salebrosa* (Piper) Jones **[G,W,H,T]** 6500–8360′; JAC, PPH, TET, YEL **[25]** bua, mmc, mog, scs, str, wet, wib.
Solidago missouriensis Nutt. var. *missouriensis* **[G,W]** 6743–7186′; JAC, YEL **[5]** mmm, mmc, sas, sps.
Solidago multiradiata Ait. var. *scopulorum* A. Gray **[G,W,H]** 6560–11320′; JAC, PPH, TET, YEL **[33]** alt, clf, mm, mmc, mos, sum, sps, wib.
▲● *Sonchus arvensis* L ssp. *arvensis* **[T]** 7340′; YEL **[1]** dis.
◄● *Sonchus arvensis* L. ssp. *uliginosus* (M. Beib.) Nyman **[G]** 6935′; JAC **[1]** str. [*Sonchus uliginosus* Bieb.]
Stenotus acaulis (Nutt.) Nutt. **[G]** 6560–10000′; JAC, TET **[5]** alt, sps.
< *Stephanomeria fluminea* Gottlieb **[H]** 7220–7250′; PPH **[2]** scs.
Symphyotrichum ascendens (Lindl.) G.L. Nesom **[G,W,H,T]** 6527–8880′; JAC, PPH, TET, YEL **[8]** mm, mog, scs, sps, wet.
Symphyotrichum campestre (Nutt.) G.L. Nesom **[G]** 7785′; TET **[1]** sps, tas.
Symphyotrichum cusickii (A. Gray) G.L. Nesom **[G]** 8760–9300′; TET **[1]** mm.
Symphyotrichum eatonii (A. Gray) G.L. Nesom **[G,W,H,T]** 6460–6840′; JAC, PPH, YEL **[9]** dis, sas, scs, wet.
Symphyotrichum foliaceum (Lindl. ex DC.) G.L. Nesom var. *apricum* (A. Gray) G.L. Nesom **[G,H]** 6700–8320′; JAC, PPH **[4]** dis, mm, scs, wib.
Symphyotrichum foliaceum (Lindl. ex DC.) G.L. Nesom var. *canbyi* (A. Gray) G.L. Nesom **[G,W,H]** 7155–9680′; PPH, TET, YEL **[9]** alt, mmc, mog, scs, sps, wib.
Symphyotrichum foliaceum (Lindl. ex DC.) G.L. Nesom var. *parryi* (D.C. Eaton) G.L. Nesom **[G,H,T]** 6491–10600′; JAC, PPH, TET, YEL **[18]** aqu, mm, mmm, mmc, str, wet, wib.
Symphyotrichum spathulatum (Lindl.) G.L. Nesom var. *spathulatum* **[G,W,H,T]** 6460–8360′; JAC, PPH, TET, YEL **[14]** mmm, mmc, scs, str, wet.
Symphyotrichum welshii (Cronq.) G.L. Nesom **[W,H,T]** 6333–7780′; PPH, YEL **[4]** mmm, str, wet.
▲● *Tanacetum vulgare* L. **[G]** 6880′; JAC **[1]** dis.
● *Taraxacum laevigatum* (Willd.) DC. **[G,H]** 6550′; JAC, PPH, TET **[19]** asf, dis, mm, mmc, mog, sas.
Taraxacum lyratum (Ledeb.) DC. **[G]** 10000′; TET **[1]** sps, tas. [*Taraxacum scopulorum* (A. Gray) Rydb.]
● *Taraxacum officinale* F.H. Wigg. ssp. *officinale* **[G,H]** 6400–8640′; JAC, PPH, TET **[10]** mm, mmm, sas, mmc, str.
► *Taraxacum officinale* F.H. Wigg. ssp. *ceratophorum* (Ledeb.) Schinz ex Thell. **[G]** 10600′; TET **[1]** alt, tas. [*Taraxacum ceratophorum* (Ledeb.) DC.]
Tetraneuris grandiflora (T. & G. ex A. Gray) Parker **[G]** 9607–

10875'; TET **[3]** alt, clf, tas. [*Hymenoxys grandiflora* (T. & G. ex A. Gray) Parker]

Townsendia alpigena Piper var. *alpigena* **[G,H]** 8160–10000'; PPH, TET **[7]** alt, sum, sps, tas.

Townsendia parryi D.C. Eat. **[G]** 9300–9565'; TET **[2]** alt, sum, sps.

● *Tragopogon dubius* Scop. **[G,H]** 6600–8720'; JAC, PPH, TET **[25]** bua, dis, mm, mmc, mos, sas, scs, sps, wib.

● *Tragopogon lamottei* Rouy **[G,W]** 6820–8400'; JAC, TET, YEL **[4]** dis, scs, sum, wet.

● *Tripleurospermum maritimum* (L.) W.D.J. Koch ssp. *maritimum* **[G]** 6573'; JAC **[1]** dis. [*Matricaria maritima* L. ssp. *maritima*]

Wyethia amplexicaulis (Nutt.) Nutt. **[G]** 6520–6686'; JAC **[3]** mm, sas.

Wyethia helianthoides Nutt. **[G]** 6850'; JAC **[1]** mmm.

Berberidaceae

Mahonia repens (Lindl.) G. Don **[G,H]** 6550–8880'; JAC, PPH, TET **[37]** bua, mm, mmm, mmc, sas, sps, tas.

Betulaceae

Alnus incana (L.) Moench ssp. tenuifolia (Nutt.) Breitung **[G,H]** 6400–7934'; JAC, PPH, TET **[11]** mmm, scs, str. [*Alnus incana* var. *occidentalis* (Dippel) C.L. Hitchc.]

Betula glandulosa Michx. **[G,W,H,T]** 6333–8985'; JAC, PPH, TET, YEL **[16]** mmm, mmc, scs, str, wet, wib.

Boraginaceae

● *Asperugo procumbens* L. **[H]** 7000'; JAC **[1]** dis.

Cryptantha ambigua (A. Gray) Greene **[G,H]** 6600–8320'; JAC, PPH **[4]** mmm, mos, sas, sps.

Cryptantha torreyana (A. Gray) Greene var. *torreyana* **[G]** 6560–7340'; JAC, TET **[7]** dis, mm, mmc, mos.

▲● *Cynoglossum officinale* L. **[G]** 6550–6845'; JAC **[4]** sas, str.

Hackelia floribunda (Lehm.) I. M. Johnst. **[G,H]** 6920–9060'; JAC, PPH, TET **[11]** bua, mm, mmm.

Hackelia patens (Nutt.) I. M. Johnst. var. *patens* **[G]** 6550–8000'; JAC, TET **[17]** mmm, mmc, mos, sps.

Lappula occidentalis (S. Watson) Greene var. *occidentalis* **[G,H]** 6400–7000'; JAC **[8]** dis, sas, sps. [*Lappula redowskii* (Hornem.) Greene var. *redowskii*]

◄● *Lappula squarrosa* (Retz.) Dumort. **[G]** 6600–7000'; JAC **[3]** dis, mmm, mog, sps.

Lithospermum ruderale Dougl. ex Lehm. **[G,H]** 6232–7000'; JAC, PPH, TET **[26]** dis, mm, mmc, mos, sas, sum, sps.

Mertensia ciliata (James ex Torr.) G. Don var. *ciliata* **[G,W,H]** 6594–9240'; JAC, PPH, TET **[27]** mm, mmm, mmc, str, wib.

Plagiobothrys scouleri (H. & A.) I. M. Johnst. var. *hispidulus* (Greene) Dorn **[G,H]** 6880–8680'; PPH, TET **[2]** mmm.

Brassicaceae

● *Alyssum alyssoides* (L.) L. **[G]** 6400–6938'; JAC **[2]** sps, str.

● *Alyssum desertorum* Stapf **[G,H]** 6400–7180'; JAC **[9]** bua, mm, mog, sas, str, wib.

Arabis drummondii A. Gray **[G,H]** 6550–10600'; JAC, PPH, TET **[52]** alt, asf, bua, mm, mmc, mog, mos, sas, sum, scs, sps, str. [*Boechera angustifolia* (Nutt.) Dorn] [*Boechera brachycarpa* (T. & G.) Dorn)]

Arabis glabra (L.) Bernh. var. *glabra* **[G,H]** 6750–8100'; JAC, PPH, TET **[18]** bua, mm, mmm, mmc, sas, sps.

Arabis hirsuta (L.) Scop. var. *glabrata* T. & G. **[H]** 8400'; PPH **[1]** sum.

Arabis hirsuta (L.) Scop. var. *pycnocarpa* (M. Hopk.) Roll. **[G]** 6780–7350'; JAC, TET **[5]** str, wib.

Arabis holboellii Hornem. var. *collinsii* (Fernald.) Roll. **[G]** 6700–6800'; JAC **[1]** sps. [*Boechera holboellii* (Hornem.*)* Löve & Löve var. *collinsii* (Fern.) Dorn]

Arabis holboellii Hornem. var. *pendulocarpa* (A. Nelson) Roll. **[G,H]** 6880–8915'; JAC, PPH, TET **[4]** mm, mmm, mmc. [*Boechera exilis* (A. Nels.) Dorn]

Arabis holboellii Hornem. var. *pinetorum* (Tidest.) Roll. **[G,H]** 6600–8280'; JAC, PPH, TET **[9]** sas, scs, sps. [*Boechera holboellii* (Hornem.*)* Löve & Löve var. *pinetorum* (Tidestr.) Dorn]

Arabis holboellii Hornem. var. *retrofracta* (Graham) Rydb. **[G,H]** 6400–9200'; JAC, PPH, TET **[47]** asf, dis, mmm, mmc, mos, scs, sps. [*Boechera holboellii* (Hornem.*)* Löve & Löve var. *secunda* (Howell.) Dorn]

Arabis lemmonii Wats. var. *lemmonii* **[G]** 8878–10600'; TET **[5]** alt, smc, sps. *Arabis lignifera* A. Nels. **[H]** 7000'; JAC **[1]** sps. [*Boechera lignifera* (A. Nels.) Weber]

Arabis lyallii Wats. var. *lyallii* **[G]** 9590–10640'; TET **[6]** alt, sum, sps. [*Boechera lyallii* (Wats.) Dorn]

► *Arabis microphylla* Nutt. var. *microphylla* **[G,H]** 6806–10640'; JAC, PPH, TET **[8]** alt, clf, sps, tas. [*Boechera microphylla* (Nutt.) Dorn var. *microphylla*]

Arabis nuttallii Robins. **[G,H]** 6597–9300'; JAC, TET **[3]** sas, sps.

► *Arabis williamsii* Roll. var. *saximontana* (Roll.) Roll. **[G,H]** 6686–10800'; JAC, PPH, TET **[7]** alt, mmc, mm, mos, smc, sps. [*Boechera williamsii* (Rollins) Dorn var. *saximontana* (Rollins) Dorn]

Barbarea orthoceras Ledeb. **[G,W]** 6810–7360'; JAC, YEL **[2]** dis, mmm.

Berteroa incana (L.) DC. **[G]** 6400'; JAC **[1]** scs.

◄● *Camelina microcarpa* Andrz. ex DC. **[G]** 6560'; JAC **[1]** bua.

● *Capsella bursa-pastoris* (L.) Medik. **[G,H]** 6479–6900'; JAC **[7]** dis, mmm, sas, str, wib.

Cardamine breweri Wats. var. *breweri* **[G,H]** 6680–8360'; JAC, PPH, TET **[4]** mm, wet, wib.

Cardamine pensylvanica Muhl. ex Willd. **[G,H,T]** 6400–8320'; JAC, PPH, YEL **[6]** aqu, mm, mmm, str.

● *Chorispora tenella* (Pall.) DC. **[G]** 6852'; JAC **[1]** dis.

Descurainia californica (A. Gray) O. E. Schulz **[G,H]** 6800–7366'; JAC, PPH, TET **[4]** bua, mm, mmc.

Descurainia incana (Bernh. ex Fisch. & Mey.) Dorn ssp. *incana* **[H]** 7280–8130'; PPH, TET **[2]** mmc, scs. [*Descurainia incana* var. *major* (Hook.) Dorn]

Descurainia incana (Bernh. ex Fisch. & Mey.) Dorn ssp. *procera* (Greene) Kartesz & Gandhi **[G,H]** 7350–9620'; PPH, TET **[6]** mm, sum, sps, wib. [*Descurainia incana* var. *macrosperma* (O. E. Schulz) Dorn]

Descurainia incana (Bernh. ex Fisch. & Mey.) Dorn ssp. *viscosa* (Rydb.) Kartesz & Gandhi **[G]** 7200'; TET **[1]** mm. [*Descurainia incana* var. *viscosa* (Rydb.) Dorn]

Descurainia pinnata (Walt.) Britt. ssp. *nelsonii* (Rydb.) Detling **[G]** 6597–7000'; JAC **[6]** bua, mmc, sas, sps. [*Descurainia pinnata* var. *nelsonii* (Rydb.) Peck]

< *Descurainia pinnata* (Walt.) Britt. ssp. *paysonii* Detl. **[G]** 6686';

JAC **[1]** mmc, str. [*Descurainia pinnata* var. *paysonii* (Detl.) Welsh & Reveal]

● *Descurainia sophia* (L.) Webb ex Prantl **[G,H]** 6686–6900′; JAC, PPH **[3]** mmc, mos, sps.

Draba albertina Greene **[G,H]** 6607–8275′; JAC, PPH, TET, YEL **[13]** mm, mmm, mmc.

Draba aurea Vahl ex Hornem. **[G]** 8770–10255′; TET **[4]** alt, smc, sps.

► *Draba breweri* Wats. var. *cana* (Rydb.) Roll. **[G]** 8500–9740′; TET **[5]** alt, sps. [*Draba cana* Rydb.]

◄ *Draba crassa* Rydb. **[G,H]** 8680–10640′; PPH, TET **[6]** alt, clf, sum, tas.

◄ *Draba fladnizensis* Wulf. var. *pattersonii* (O. E. Schulz) Roll. **[G]** 9530′; TET **[1]** sps, tas. [*Draba fladnizensis*]

► *Draba incerta* Pays. **[G]** 9800′; TET **[1]** sps, tas.

Draba lonchocarpa Rydb. var. *lonchocarpa* **[G]** 8878–11320′; TET **[9]** alt, clf, sps, tas.

Draba nemorosa L. **[G,H]** 6479–8320′; JAC, PPH, TET **[6]** mm, mmm, mmc, sas, str.

Draba oligosperma Hook. **[G]** 9300–10000′; TET **[7]** alt, sps, tas.

► *Draba praealta* Greene **[G]** 6597–9320′; JAC, TET **[4]** clf, sps, tas.

► *Draba reptans* (Lam.) Fern. **[G]** 6560–6852′; JAC **[2]** bua, dis.

Erysimum capitatum (Dougl. ex Hook.) Greene var. *capitatum* **[G]** 6800–9640′; TET **[14]** mm, mmc, mos, sum, sps. [*Erysimum asperum* (Nutt.) DC. var. *arkansanum* (Nutt.) A. Gray]

● *Erysimum cheiranthoides* L. **[G]** 6680′; JAC **[1]** dis, mmm.

Erysimum inconspicuum (Wats.) MacM. **[G,H]** 6900–6865′; JAC **[2]** mos, sps.

● *Lepidium campestre* (L.) W.T. Aiton **[G]** 6560–7000′; JAC **[4]** bua, dis, mm.

Lepidium densiflorum Schrad. var. *densiflorum* **[G]** 6760′; JAC **[1]** dis.

Lepidium densiflorum Schrad. var. *macrocarpum* Mulligan **[G,H]** 6743–7000′; JAC **[6]** asf, dis, mmc.

Lepidium densiflorum Schrad. var. *pubecarpum* (A. Nels.) Thell. **[G]** 6560′; JAC **[1]** bua. [*Lepidium densiflorum* var. *pubicarpum* (A. Nels.) Thell.]

● *Lepidium perfoliatum* L. **[G]** 6400–6560′; JAC **[2]** bua, scs.

Lepidium ramosissimum A. Nels. **[H]** 7220′; PPH **[1]** scs.

◄ *Lepidium virginicum* L. var. *pubescens* (Greene) Thell. **[G]** 6400–7220′; JAC, TET **[8]** dis, mos, sas, scs, sps.

< *Lesquerella carinata* var. *carinata* Roll. **[G,H]** 7000–8400′; JAC, TET **[4]** mm, sum, sps.

◄ *Lesquerella paysonii* Roll. **[G]** 9800′; TET **[1]** clf, sps, tas.

● *Nasturtium officinale* W.T. Aiton **[G,W]** 6680–6900′; JAC, YEL **[2]** str, wet.

Noccaea montana (L.) F.K. Mey. var. *montana* **[G]** 8275–9320′; TET **[2]** clf, mm, tas. [*Thlaspi montanum* L. var. *montanum*]

Physaria didymocarpa (Hook.) A. Gray var. *didymocarpa* **[G]** 7367′; JAC **[1]** sps.

Physaria integrifolia (Roll.) Lichvar var. *integrifolia* **[G]** 6900–7160′; JAC **[1]** sps.

Rorippa alpina (Wats.) Rydb. **[G]** 10100–10640′; TET **[2]** alt, mmc. [*Rorippa curvipes* Greene var. *alpina* (Wats.) Stuckey]

Rorippa curvipes Greene var. *curvipes* **[G]** 6680–7000′; JAC **[2]** mm, mmm, wet.

Rorippa curvipes Greene var. *truncata* (Jeps.) Rollins **[H]** 7220′; PPH **[1]** scs. [*Rorippa truncata* (Jeps.) Stuckey]

Rorippa curvisiliqua (Hook.) Besser ex Britt. var. *curvisiliqua* **[H]** 7920′; PPH **[1]** dis.

Rorippa curvisiliqua (Hook.) Besser ex Britt. var. *orientalis* Stuckey **[H]** 7980′; PPH **[1]** dis.

Rorippa palustris (L.) Bess. var. *fernaldiana* (Butters & Abbe) Stuckey **[G]** 6563′; JAC **[1]** aqu.

Rorippa palustris (L.) Bess. ssp. *hispida* (Desv.) Johnsell. **[G,T]** 6400′; JAC, YEL **[2]** mmm, wet. [*Rorippa palustris* var. *elongata* Stuckey] [*Rorippa palustris* var. *hispida* (Desv.) Rydb.]

► *Schoenocrambe linifolia* (Nutt.) Greene **[G]** 6597′; JAC **[2]** sps.

● *Sisymbrium altissimum* L. **[G]** 6932–6400′; JAC **[2]** sps, scs.

Smelowskia calycina (Steph. ex Willd.) C. A. Mey. var. *americana* (Regel & Herd.) Drury & Roll. **[G]** 9300–10800′; TET **[8]** alt, sps, tas.

● *Thlaspi arvense* L. **[G,H]** 6520–7000′; JAC **[11]** dis, mm, mmm.

Cactaceae

Opuntia fragilis (Nutt.) Haw. var. *fragilis* **[G]** 6400–6800′; JAC **[2]** sps.

Callitrichaceae

Callitriche hermaphroditica L. **[G]** 7200′; JAC **[1]** aqu.

Callitriche heterophylla Pursh var. *heterophylla* **[T]** 7340′; YEL **[1]** mmc.

Callitriche palustris L. **[G,W]** 6680–10100′; JAC, PPH, TET **[5]** aqu.

Campanulaceae

Campanula rotundifolia L. **[G,W,H,T]** 6700–10480′; JAC, PPH, TET, YEL **[35]** bua, mm, mmc, mog, mos, sum, scs, sps, wib.

► *Campanula uniflora* L. **[G]** 10255′; TET **[1]** alt.

> *Porterella carnosula* (H. & A.) Torr. **[G]** 6860′; JAC **[1]** wet.

Cannabaceae

Humulus lupulus L. var. *neomexicanus* Nels. & Ckll. **[G]** 6760′; JAC **[1]** dis.

Caprifoliaceae

►●× *Lonicera* ×*bella* Zabel **[G]** 6760′; JAC **[1]** dis.

Lonicera involucrata (Richards.) Banks ex Spreng. var. *involucrata* **[G,W,H,]** 6573–8375′; JAC, PPH, TET, YEL **[38]** mmm, scs, str, wet, wib.

Lonicera utahensis Wats. **[G,W,H,T]** 6607–9200′; JAC, PPH, TET, YEL **[35]** mm, mmc, mos, str, wet.

Sambucus racemosa L. var. *racemosa* **[G,W,H]** 6573–8775′; JAC, PPH, TET **[5]** mm, mmc, tas. [*Sambucus racemosa* var. *microbotrys* (Rydb.) Kearn. & Peeb.]

Sambucus racemosa L. var. *melanocarpa* (A. Gray) McMinn **[H]** 7740′; PPH **[1]** mm, mmc.

Symphoricarpos occidentalis Hook. **[G]** 7366′; TET **[1]** mog.

Symphoricarpos oreophilus A. Gray var. *utahensis* (Rydb.) A. Nels. **[G,W]** 6232–8915′; JAC, PPH, TET, YEL **[18]** bua, dis, mm, mmc, smc, tas.

Caryophyllaceae

Arenaria congesta Nutt. var. *congesta* **[G,W,H]** 6560–10795′; JAC, PPH, TET, YEL **[34]** alt, clf, dis, mm, mmc, sas, sps. [*Eremogone congesta* (Nutt.) Ikonnikov var. *congesta*]

Cerastium arvense L. **[G,W,H]** 6520–7400′; JAC, PPH, TET, YEL **[18]** mm, mmm, mmc, mos, sas, scs, wib.

Cerastium beeringianum Cham. & Schlecht. var. *earlei* (Rydb.) Hulten **[G]** 10000–10390′; TET **[2]** tas. [*Cerastium beeringianum*. var. *capillare* Fern. & Wieg.]

● *Cerastium fontanum* Baumg. ssp. *vulgare* (Hartm.) Greuter & Burdet **[G,W,H,T]** 6680–7350′; JAC, PPH, TET, YEL **[13]** mmm, mmc, sas, scs, str, wet, wib. [*Cerastium fontanum*]

◄ *Minuartia austromontana* S. J. Wolf & Packer **[G]** 10198–10795′; TET **[2]** alt.

◄>*Minuartia macrantha* (Rydb.) House **[G]** 9140′; TET **[1]** alt. [*Minuartia filiorum* (Maguire) McNeil]

Minuartia nuttallii (Pax) Briq. ssp. *nuttallii* **[G]** 8160–9640′; TET **[3]** sum, smc, tas.

Minuartia obtusiloba (Rydb.) House **[G]** 8600–10800′; TET **[16]** alt, clf, str, tas.

◄ *Minuartia rubella* (Wahlenb.) Hiern **[G]** 8878–10255′; TET **[8]** alt, clf, sum, smc, tas.

Moehringia lateriflora (L.) Fenzl **[G,H,T]** 6460–7185′; JAC, TET, YEL **[10]** mmc, mog, sas, str, wib.

Sagina saginoides (L.) Karst. **[G,W,H,]** 6780–10640′; JAC, PPH, TET, YEL **[18]** alt, clf, dis, sum, scs, wet, wib.

Silene acaulis (L.) Jacq. var. *subacaulescens* (F. N. Wms.) Fern. & St John **[G]** 9400–11320′; TET **[8]** alt, clf, tas.

► *Silene drummondii* Hook. var. *drummondii* **[G]** 6800–7340′; JAC, TET **[2]** bua, mm, mos.

● *Silene latifolia* Poir. ssp. *alba* (Mill.) Greuter & Burdet **[G,W]** 6400–6840′; JAC, YEL **[2]** wet. [*Silene latifolia*]

Silene menziesii Hook. **[G,H]** 6560–7360′; JAC, PPH **[7]** bua, dis, scs. [*Silene menziesii* var. *menziesii*] [*Silene menziesii* var. *viscosa* (Greene) Hitchc. & Maguire]

Silene oregana Wats. **[G,H]** 7200–8450′; PPH, TET **[2]** mm, mmc.

Silene parryi (Wats.) Hitchc. & Maguire **[G]** 7840–9680′; TET **[7]** mm, mmc, sum.

● *Spergularia rubra* (L.) J. & K. Presl **[G,W,H]** 6700–7000′; JAC, YEL **[5]** dis, mmm.

Stellaria calycantha (Ledeb.) Bong. **[W,H]** 7020–8320′; PPH, YEL **[7]** mm, mmm, str, wet.

> *Stellaria crispa* Cham. & Schlecht. **[G,T]** 6527–8975′; JAC, TET, YEL **[3]** str, wet.

Stellaria longifolia Muhl. ex Willd. **[G,W,H]** 6680–7580′; JAC, PPH, TET, YEL **[6]** mmm, str, wet, wib.

Stellaria longipes Goldie ssp. *longipes* **[G,W,H]** 6760–8320′; JAC, PPH, TET, YEL **[25]** asf, bua, mmm, scs, sps, str, wet, wib.

Stellaria obtusa Engelm. **[G,H]** 6760–8885′; JAC, PPH, TET **[9]** mmm, mmc, scs, wib.

Stellaria umbellata Turcz. ex Karel. & Kir. **[G,H]** 7580–10640′; JAC, PPH, TET **[13]** alt, clf, mm, mmm, sum, tas, wet.

Celastraceae

Paxistima myrsinites (Pursh) Raf. **[G,H]** 6597–8953′; JAC, PPH, TET **[17]** bua, mm, mmc, tas.

Ceratophyllaceae

Ceratophyllum demersum L. **[T]** 6333–6400′; YEL **[1]** wet.

Chenopodiaceae

Chenopodium atrovirens Rydb. **[G]** 6760–9060′; JAC, TET **[4]** dis, mm, mmc, sps.

Chenopodium capitatum (L.) Asch. **[G]** 7366′; TET **[1]** bua.

Chenopodium foliosum (Moench) Asch. **[G,H]** 6597–7220′; JAC, PPH **[3]** dis, scs, sps. [*Chenopodium capitatum* (L.) Asch. var. *parvicapitatum* S.L. Welsh]

Clusiaceae

Hypericum scouleri Hook. ssp. *scouleri* **[G,W,H]** 6900–10060′; PPH, TET, YEL **[7]** mm, str, tas, wet. [*Hypericum formosum* var. *formosum*] [*Hypericum formosum* var. *scouleri* (Hook.) Coult.]

Cornaceae

Cornus sericea L. ssp. *sericea* **[G]** 6573–7200′; JAC, TET **[7]** str.

Crassulaceae

Rhodiola integrifolia (Raf.) ssp. *integrifolia* **[G]** 10000–10480′; TET **[2]** alt, clf, sum. [*Sedum integrifolium* (Raf.) A. Nels.]

Rhodiola rhodantha (A. Gray) H. Jacobsen **[G]** 7840–10305′; TET **[3]** alt, sum, str, wib. [*Sedum rhodanthum* A. Gray]

Sedum debile Wats. **[G]** 9240–10480′; TET **[5]** alt, clf, sum.

Sedum lanceolatum Torr. var. *lanceolatum* **[G,H]** 6400–10350′; JAC, PPH, TET **[21]** alt, clf, dis, mmc, sas, sum, tas.

Cyperaceae

Carex aquatilis Wahlenb. var. *aquatilis* **[G,W,H,T]** 6460–9180′; JAC, PPH, TET, YEL **[29]** str, wet, wib.

Carex athrostachya Olney **[G,T]** 6400–6900′; JAC, YEL **[5]** aqu, mog, str.

Carex aurea Nutt. **[G,W,H]** 6820–7780′; JAC, PPH, TET, YEL **[16]** mmm, scs, str, wet, wib.

◄ *Carex bebbii* Olney ex. Fern. **[G]** 6680′; JAC **[1]** mmm.

Carex buxbaumii Wahlenb. **[W,T]** 6460–7160′; YEL **[2]** mmm, str.

< *Carex cusickii* Mack. ex Piper & Beattie **[W,H]** 6840–7300′; YEL **[4]** str, wet.

Carex disperma Dewey **[G,H]** 6840–7560′; JAC, PPH **[4]** str, wet, wib.

Carex douglasii Boott **[G]** 6398′; JAC **[1]** scs, wib.

Carex duriuscula C. A. Mey. **[G,H]** 7000–7550′; JAC, PPH **[2]** sps, wet. [*Carex stenophylla* Wahlenb.]

>*Carex echinata* J. A. Murray ssp. *echinata* **[G,W,H,T]** 6460–7539′; JAC, TET, YEL **[5]** mmm, str.

Carex elynoides Holm **[G]** 8600–10800′; TET **[7]** alt, tas.

Carex engelmannii L.H. Bailey **[G]** 9400–10795′; TET **[4]** alt, tas. [*Carex breweri* Boott var. *paddoensis* (Suksd.) Cronq.]

Carex filifolia Nutt. **[G]** 6560′; JAC **[1]** bua.

Carex geyeri Boott **[G,W,H]** 6920–9267′; JAC, PPH, TET, YEL **[36]** asf, bua, mm, mmc, mog, mos, sas, tas.

Carex haydeniana Olney **[G,H]** 6900–10795′; JAC, PPH, TET **[7]** alt, mmm, tas.

Carex hoodii Boott **[G,H]** 6520–8915′; JAC, PPH, TET, YEL **[43]** bua, mm, mmc, sas, sum, sps, wib.

Carex illota Bailey **[G,H]** 8320–9240′; PPH, TET **[3]** mmm, str.

►< *Carex incurviformis* Mack. var. *danaensis* (Stacey) F. J. Herm. **[G]** 10600′; TET **[1]** alt.

Carex interior Bailey **[G]** 6816–7840′; JAC, TET **[2]** mmc, str.

► *Carex lachenalii* Schkuhr. **[G]** 10100–10390′; TET **[3]** alt, smc, tas. [*Carex bipartita* All.]

Carex lapponica O.F.Lang **[G,W,H]** 6900–8065′; JAC, PPH, YEL **[8]** mmm, str, wet. [*Carex canescens* L.]

Carex lasiocarpa Ehrh. **[G]** 6500′; YEL **[1]** wet.

Carex lenticularis Michx. var. *lipocarpa* (T. Holm) L.A. Standl. **[G]** 6816–7840′; JAC, TET **[5]** mmc, str, wet, wib. [*Carex lenticularis* var. *pallida* (Boott) Dorn]

◄ *Carex leptalea* Wahlenb. **[G]** 6854′; TET **[1]** mmc, str.

< *Carex limosa* L. **[W,T]** 6460–7340′; YEL **[5]** mmm, mmc, wet.

►< *Carex livida* (Wahlenb.) Willd. var. *radicaulis* Paine **[W]** 6980′; YEL **[1]** str. [*Carex livida*]

Carex luzulina Olney var. *ablata* (Bailey) F. J. Herm. **[G,W,T]** 6816–8065′; JAC, TET, YEL **[7]** mmm, mmc, str, wet.

► *Carex macloviana* Urv. **[G]** 8975–11320′; TET **[6]** alt, mm, sps, tas.

Carex microptera Mack. **[G,W,H]** 6816–8680′; JAC, PPH, TET, YEL **[16]** mm, mmm, scs, str, wib. [*Carex microptera* var. *microptera*] [*Carex microptera* var. *limnophila* (F. J. Herm.) Dorn]

Carex nardina Fries **[G,H]** 10000–10795′; TET **[5]** alt.

Carex nebrascensis Dewey **[G,W,T]** 6573–7340′; JAC, YEL **[6]** mmc, mmm, str, wib.

Carex neurophora Mack. **[G,H]** 7580–8320′; PPH, TET **[3]** mmm, wib.

Carex nigricans C. A. Mey. **[G]** 9240–10100′; TET **[2]** alt, smc.

Carex norvegica Retz. ssp. *stevenii* (Holm) E. Murray **[G]** 7090′; TET **[1]** str. [*Carex norvegica* var. *stevenii* (Holm) Dorn]

◄ *Carex pachystachya* Cham. ex Steud. **[G,H]** 7680–11320′; PPH, TET **[9]** alt, mmm, scs, tas, wet, wib.

Carex paysonis Clokey **[G]** 9590–11320′; TET **[4]** alt, tas.

◄ *Carex pellita* Muhl. ex Willd. **[G,W,T]** 6460–6845′; JAC, YEL **[5]** mmm, wet.

Carex pelocarpa F.J. Herm. **[G]** 9760–10795′; TET **[2]** alt. [*Carex nova* Bailey var. *pelocarpa* (F. J. Herm.) Dorn]

Carex petasata Dewey **[G]** 6700–7160′; JAC **[4]** bua, sas.

Carex phaeocephala Piper **[G]** 6975–11320′; JAC, TET **[5]** alt, mmm, tas.

► *Carex platylepis* Mack. **[G]** 6816–7680′; JAC, TET **[2]** str.

Carex praeceptorum Mack. **[G,H]** 7255–10100′; PPH, TET **[2]** mm, smc.

Carex praticola Rydb. **[G]** 6880′; JAC **[1]** mmm.

►> *Carex proposita* Mack. **[G]** 9607′; TET **[1]** wet.

Carex pyrenaica Wahlenb. **[G]** 10060–10640′; TET **[3]** alt, clf, tas.

Carex raynoldsii Dewey **[G,H]** 6930–9130′; JAC, PPH, TET, YEL **[13]** asf, mm, mmc, mos, sas.

Carex rossii Boott **[G,H]** 6573–9615′; JAC, PPH, TET, YEL **[18]** mm, mmc, sas, sum, str, tas.

► *Carex scopulorum* Holm var. *scopulorum* **[G]** 9240′; TET **[1]** sum.

◄ *Carex simulata* Mack. **[G,W]** 6680–6840′; JAC, YEL **[3]** aqu, wet.

◄ *Carex spectabilis* Dewey **[G,H]** 8270–10640′; PPH, TET **[3]** alt, mm, tas.

Carex stenoptila F. J. Herm. **[H]** 7580–8400′; PPH **[2]** mm, mmm.

Carex utriculata Boott **[G,W,H,T]** 6400–8400′; JAC, PPH, TET, YEL **[25]** aqu, mmm, wet.

Carex vallicola Dewey var. *vallicola* **[G,H]** 6398–7367′; JAC **[6]** bua, sps, str.

Carex vesicaria L. var. *vesicaria* **[G,W,H]** 6880–8360′; JAC, PPH, TET, YEL **[9]** mmm, str, wet.

◄ *Carex viridula* Michx. var. *viridula* **[G,W,T]** 6900–7340′; JAC, YEL **[3]** str, wet.

Cyperus squarrosus L. **[G]** 6860′; JAC **[1]** wet.

Eleocharis acicularis (L.) R. & S. **[W,H,T]** 6400–8680′; PPH, YEL **[5]** mmm, wet. *Eleocharis flavescens* (Poir.) Urban var. *thermalis* (Rydb.) Cronq. **[W]** 6840′; YEL **[1]** str, wet.

Eleocharis palustris (L.) R. & S. **[G,W,H,T]** 6491–7550′; JAC, PPH, YEL **[11]** aqu, mmm, str, wet.

Eleocharis quinqueflora (Hartmann) O. Schwarz **[G,W]** 6563–6859′; JAC, YEL **[2]** mmm, str. [*Eleocharis pauciflora* (Lightf.) Link]

Eleocharis rostellata (Torr.) Torr. **[W]** 6905′; YEL **[1]** str.

◄ *Eriophorum angustifolium* Honck. ssp. *angustifolium* **[W,T]** 6500–7160′; YEL **[3]** mmm, str, wet.

< *Eriophorum gracile* Koch var. *gracile* **[T]** 6500–7340′; YEL **[2]** mmm, wet.

Scheonoplectus acutus (Muhl. ex Bigelow) A. Löve & D. Löve var. *acutus* **[T]** 6460–6527′; YEL **[2]** mmm, wet.

< *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller **[W]** 6859–6905′; YEL **[2]** str, wet.

Schoenoplectus tabernaemontani (C.C. Gmel.) Palla **[W]** 6680′; JAC **[1]** wet.

Droseraceae

< *Drosera anglica* Huds. **[W,T]** 6460–7340′; YEL **[9]** mmm, str, wet.

Elaeagnaceae

Elaeagnus commutata Bernh. ex Rydb. **[G]** 6560–8500′; JAC, TET **[5]** bua, str, sps.

Shepherdia canadensis (L.) Nutt. **[G,W,H,T]** 6500–8400′; JAC, PPH, TET, YEL **[41]** mm, mmc, sps, str.

Ericaceae

Arctostaphylos uva-ursi (L.) Spreng. **[G,W,H]** 6865–10000′; JAC, PPH, TET, YEL **[5]** mmc, sps. [*Arctostaphylos uva-ursi* var. *stipitata* (Packer & Denford) Dorn] [*Arctostaphylos uva-ursi* var. *uva-ursi*]

Chimaphila umbellata (L.) Barton ssp. *occidentalis* (Rydb.) Hulten **[G,W]** 6852–7670′; JAC, TET, YEL **[3]** mmc. [*Chimaphila umbellata* var. *occidentalis* (Rydb.) Blake]

Gaultheria humifusa (Grah.) Rydb. **[G,W,H,T]** 6980–9240′; PPH, TET, YEL **[7]** mmm, mmc.

Kalmia microphylla (Hook.) Heller **[G,W,H]** 6980–10305′; TET, YEL **[8]** alt, mmm, mmc, str.

Menziesia ferruginea Sm. **[G,H]** 6852–9267′; JAC, PPH, TET **[7]** mmc, str. [*Menziesia ferruginea* var. *glabella* (A. Gray) Peck]

Moneses uniflora (L.) A. Gray **[W]** 7280′; YEL **[1]** mmc, str.

Orthilia secunda (L.) House **[G,W,T]** 6460–10450′; JAC, TET, YEL **[10]** mmm, mmc, str.

Phyllodoce empetriformis (Sw.) D. Don **[G]** 8975–10295′; TET **[4]** alt, sum, sps.

Phyllodoce glanduliflora (Hook.) Cov. **[G]** 9680–10305′; TET **[4]** alt, sps, wet.

Pterospora andromedea Nutt. **[G,W]** 6868–7344′; JAC, YEL **[3]** mmc.

Pyrola asarifolia Michx. var. *asarifolia* **[G,W,H,T]** 6824–7340′; JAC, PPH, TET, YEL **[10]** mmm, mmc, scs, str, wet, wib.

Pyrola chlorantha Sw. **[G]** 6852–6854′; TET **[3]** mmc, str.

Pyrola minor L. **[G,T]** 6980–7340′; JAC, YEL **[2]** mm, mmc.

Vaccinium cespitosum Michx. **[G,W,T]** 7020–7760′; TET, YEL **[3]** mmc.

Vaccinium membranaceum Dougl. ex Torr. **[G,H]** 6575–9189'; JAC, PPH, TET **[23]** alt, mm, mmc, smc, str.

Vaccinium scoparium Leib. ex Cov. **[G,W,H,T]** 6600–10295'; JAC, PPH, TET, YEL **[32]** alt, bua, clf, mm, mmc, smc, sps.

Vaccinium uliginosum L. **[G,W,T]** 6491–10250'; TET, YEL **[5]** alt, mmm, mmc, wet. [*Vaccinium occidentale* A. Gray]

Euphorbiaceae

► *Chamaesyce glyptosperma* (Engelm.) Small **[W]** 6820'; YEL **[1]** str.

Fabaceae

Astragalus agrestis Dougl. ex G. Don **[G,H]** 6470–7740'; JAC, PPH, TET **[9]** mm, mmm, mmc, mos, sas, sps, wib.

Astragalus alpinus L. var. *alpinus* **[G,W,H]** 6800–9740'; JAC, PPH, TET, YEL **[23]** mm, mmm, mmc, scs, sps, str, wib.

Astragalus argophyllus Nutt. var. *argophyllus* **[G]** 6640–7367'; JAC **[5]** mm, sas, sps.

Astragalus australis (L.) Lam. **[G]** 9300'; TET **[1]** alt.

► *Astragalus convallarius* Greene var. *convallarius* **[G]** 6560'; JAC **[1]** bua.

Astragalus eucosmus Robins. **[G]** 6820'; JAC **[1]** mm.

Astragalus kentrophyta A. Gray var. *tegetarius* (Wats.) Dorn **[G,H]** 7250–10795'; PPH, TET **[14]** alt, sum, tas.

► *Astragalus laxmannii* Jacq. var. *robustior* (Hook.) Barneby & S.L. Welsh **[G]** 6950–7785'; JAC, TET **[2]** str, tas, wib.

Astragalus miser Dougl. ex. Hook. var. *hylophilus* (Rydb.) Barneby **[G,H]** 6900–8160'; JAC, PPH, TET **[9]** mmm, mmc, sps.

Astragalus miser Dougl. ex. Hook. var. *praeteritus* Barneby **[G,H]** 6398–7367'; JAC **[8]** asf, bua, sas, sps.

Astragalus miser Dougl. ex. Hook. var. *tenuifolius* (Nutt.) Barneby **[H]** 7020–7180'; JAC **[1]** sas.

◄ *Astragalus molybdenus* Barneby **[G]** 8760–10795'; TET **[3]** alt, mm.

Astragalus purshii Dougl. ex Hook. var. *purshii* **[G,H]** 6398–7160'; JAC **[5]** bua, sas, sps.

Astragalus tenellus Pursh **[G]** 6900–7367'; JAC **[3]** sps.

> *Astragalus terminalis* Wats. **[G,H]** 6640–7180'; JAC **[3]** bua, mos, sas.

Glycyrrhiza lepidota Pursh **[G]** 6680'; JAC **[1]** str. [*Glycyrrhiza lepidota* var. *glutinosa* (Nutt.) Wats.]

Hedysarum alpinum L. **[G,H]** 6885–8985'; JAC, TET **[3]** asf, mm, sum. [*Hedysarum alpinum* var. *americanum* Michx.]

Hedysarum boreale Nutt. var. *boreale* **[G]** 6900'; JAC **[1]** sps. [*Hedysarum boreale* var. *pabulare* (A. Nels.) Dorn]

Hedysarum occidentale Greene **[G]** 7210–10450'; TET **[7]** sum, smc, sps, tas.

Lupinus argenteus Pursh ssp. *argenteus* **[G,H]** 7360–9780'; JAC, PPH, TET **[5]** mm, mmm, mmc, sum, scs.

Lupinus argenteus Pursh var. *laxiflorus* (Dougl. ex Lindl.) Dorn **[G,H]** 6720–8975'; JAC, PPH, TET **[16]** bua, dis, mm, mmc, sas, sps.

Lupinus argenteus Pursh ssp. *rubricaulis* (Greene) Hess & D. Dunn **[G,H]** 6590–10600'; JAC, PPH, TET, YEL **[23]** alt, mm, mmm, mmc, sas, sps.

Lupinus caespitosus Nutt. var. *utahensis* (Wats.) Cox **[G,W,H]** 6640–8320'; JAC, PPH, YEL **[9]** mm, mmm, mmc, sas, str. [*Lupinus lepidus* Dougl. ex Lindl. var. *utahensis* (Wats.) C.L. Hitchc.]

Lupinus caudatus Kellogg ssp. *argophyllus* (A. Gray) L. Phillips **[G,W]** 6795–7155'; JAC, YEL **[2]** str. [*Lupinus argenteus* Pursh var. *argophyllus* (A. Gray) Wats.]

Lupinus depressus Rydb. **[G,H]** 8000–9680'; PPH, TET **[3]** mm, mmc, sps, tas. [*Lupinus argenteus* Pursh var. *depressus* (Rydb.) C.L. Hitchc.]

Lupinus leucophyllus Dougl. ex Lindl. **[G,H]** 6520–8000'; JAC, PPH **[5]** asf, mm, mmc, sps.

Lupinus prunophilus M.E. Jones **[G,W,H]** 6400–9530'; JAC, PPH, TET, YEL **[14]** bua, mm, mmc, sas, sps, tas. [*Lupinus polyphyllus* Lindl. var. *prunophilus* (Jones) L. Phillips]

Lupinus sericeus Pursh **[G,H]** 6400–8500'; JAC, PPH **[11]** bua, mm, mmc, sas, sps.

Lupinus wyethii S. Watson ssp. *wyethii* **[G,H]** 6880–7000'; JAC **[4]** mm, mmc, scs, sps. [*Lupinus polyphyllus* Lindl. var. *humicola* (A. Nels.) Barneby]

● *Medicago lupulina* L. **[G,W,H]** 6398–7350'; JAC, TET, YEL **[25]** bua, dis, mm, mmc, sas, scs, sps, str, wib.

● *Medicago sativa* L. **[G]** 6400–6560'; JAC **[2]** bua, mm.

● *Melilotus officinalis* (L.) Lam. **[G]** 6400'; JAC **[1]** mm. *Oxytropis borealis* DC. var. *viscida* (Nutt.) S.L. Welsh **[G]** 9665'; TET **[1]** sps, tas. [*Oxytropis viscida* Nutt. var. *viscida*]

Oxytropis campestris (L.) DC. var. *cusickii* (Greenm.) Barneby **[G]** 9300'; TET **[1]** alt.

Oxytropis deflexa (Pall.) DC. var. *foliolosa* (Hook.) Barneby **[G]** 9640–9840'; TET **[4]** sps, tas.

Oxytropis deflexa (Pall.) DC. var. *sericea* T. & G. **[G,H]** 6700–7360'; JAC, PPH **[7]** mmc, sas, scs.

● *Trifolium hybridum* L. **[G,W,H,T]** 6560–7340'; JAC, PPH, YEL **[25]** bua, dis, mm, mmm, mmc, mog, sas, scs, wib.

Trifolium longipes Nutt. ssp. *reflexum* (A. Nels.) J.M. Gillett **[G,W,H]** 6398–7360'; JAC, PPH, TET, YEL **[18]** mm, mmm, mmc, scs, str, wib.

● *Trifolium pratense* L. **[G,W,H]** 6540–7000'; JAC, PPH **[7]** mmc, sas, str.

● *Trifolium repens* L. **[G,W,H,T]** 6460–8100'; JAC, PPH, YEL **[9]** dis, mmc, sas, scs, sps.

Vicia americana Muhl. ex Willd. ssp. *minor* (Hook.) C.R. Gunn **[G]** 6398–7367'; JAC **[5]** dis, mmc, sas, sps.

Fumariaceae

Corydalis aurea Willd. **[G]** 6960'; JAC **[1]** mmc.

Dicentra uniflora Kellogg **[G,W,H]** 7320–9635'; PPH, TET, YEL **[11]** bua, mm, sas, sum, smc, sps.

Gentianaceae

Frasera speciosa Dougl. ex Griseb. **[G,H]** 6600–9300'; JAC, PPH, TET **[14]** asf, bua, mm, mmc, sas, sps.

Gentiana affinis Griseb. **[G]** 6790'; JAC **[1]** str.

Gentiana calycosa Griseb. **[G]** 7860–10795'; TET **[10]** alt, clf, sum, smc.

Gentianella amarella (L.) Borner **[G,W,H]** 6980–9060'; JAC, PPH, TET, YEL **[10]** mm, mmm, mmc, str, wib.

►> *Gentianopsis simplex* (A. Gray) Iltis **[W,H]** 6905–8360'; PPH, YEL **[2]** str, wet.

Gentianopsis thermalis (Kuntze.) Iltis **[G,W,H,T]** 6333–8360';

JAC, PPH, YEL **[18]** mmm, str, wet, wib. [*Gentianopsis detonsa* (Rottb.) Ma var. *elegans* (A. Nels.) N. Holmgren]
Swertia perennis L. **[G]** 7185′; TET **[1]** wib.

Geraniaceae

Geranium richardsonii Fisch. & Trautv. **[G,W,H]** 6770–8420′; JAC, PPH, TET, YEL **[26]** mmm, scs, str, wib.
Geranium viscosissimum Fisch. & Mey. ex Mey. var. *viscosissimum* **[G,W,H]** 6555–8320′; JAC, PPH, TET, YEL **[35]** asf, mm, mmm, mmc, mog, mos, sas.
Geranium viscosissimum Fisch. & Mey. ex Mey. var. *incisum* (Torr. & A. Gray.) N.H. Holmgren **[G,H]** 6760–8640′; JAC, PPH **[4]** mm, mmc, mos. [*Geranium viscosissimum* var. *nervosum* (Rydb.) C.L. Hitchc.]

Grossulariaceae

Ribes cereum Dougl. var. *pedicellare* Brewer & Wats. **[G,H]** 6595–8130′; JAC, PPH **[7]** mmc, sps.
Ribes hudsonianum Richards. var. *petiolare* (Dougl.) Jancz. **[G,H]** 6590–7598′; JAC, PPH, TET **[4]** mmc, str. [*Ribes hudsonianum*]
Ribes inerme Rydb. var. *inerme* **[G,H]** 6790–6920′; JAC **[3]** asf, mm, wib.
Ribes lacustre (Pers.) Poir. **[G,H]** 6600–9615′; JAC, PPH, TET, YEL **[16]** bua, mmc, mos, str.
Ribes montigenum McClat. **[G,H]** 6900–9635′; JAC, PPH, TET **[14]** alt, mm, mmc, sum, sps.
Ribes viscosissimum Pursh **[G,H]** 6760–9200′; JAC, PPH, TET, YEL **[22]** bua, mm, mmc, mos, str.

Haloragaceae

Myriophyllum sibiricum Kom. **[G,W,H]** 6820–7560′; JAC, PPH, YEL **[3]** aqu.
►> *Myriophyllum verticillatum* L. **[G]** 6790′; JAC **[1]** aqu.

Hippuridaceae

Hippuris vulgaris L. **[G,H,T]** 6400–8140′; JAC, PPH, YEL **[3]** aqu.

Hydrocharitaceae

Elodea canadensis Michx. **[T]** 7340′; YEL **[1]** aqu.

Hydrophyllaceae

Hydrophyllum capitatum Dougl. ex Benth. var. *capitatum* **[G,W,H]** 6595–8975′; JAC, PPH, TET, YEL **[26]** dis, mm, mmc, sas, sum, smc.
Nemophila breviflora A. Gray **[G,H]** 6600–8000′; JAC, PPH, TET **[28]** mm, mmc, mos, sas.
Phacelia franklinii (R. Br.) A. Gray **[G]** 6900–7000′; JAC **[1]** dis.
Phacelia hastata Dougl. ex Lehm. var. *hastata* **[G,W,H]** 6700–10480′; JAC, PPH, TET, YEL **[22]** mmc, sum, sps, tas.
Phacelia heterophylla Pursh ssp. *virgata* (Greene) Heckard **[G,H]** 6700–7200′; JAC, PPH **[6]** bua, mm, mmc, mos.
Phacelia sericea (Graham) A. Gray ssp. *sericea* **[G,H]** 6600–10600′; JAC, PPH, TET **[13]** alt, mm, mmc, mos, sum, sps.

Iridaceae

Sisyrinchium idahoense Bickn. var. *occidentale* (Bickn.) D. M. Hend. **[G,W,H]** 6700–7250′; JAC, PPH, YEL **[6]** scs, str, wet, wib.

Juncaceae

Juncus arcticus Willd. ssp. *littoralis* (Engelm.) Hulten **[G,W,H]** 6573–6905′; JAC, YEL **[6]** aqu, sps, wet. [*Juncus balticus* Willd. var. *montanus* Engelm.]
Juncus bufonius L. **[G,H]** 6680–8400′; JAC, PPH **[3]** dis, mmm, str.
Juncus confusus Cov. **[G,H,T]** 6527–8320′; JAC, PPH, TET, YEL **[8]** mm, mmm, mmc, mog, wet.
Juncus drummondii E. Mey. **[G]** 7680–10800′; TET **[10]** alt, clf, smc, tas, wib.
Juncus ensifolius Wikstr. **[G,W,H,T]** 6460–8360′; JAC, PPH, TET, YEL **[33]** aqu, mmm, mmc, str, wet, wib. [*Juncus ensifolius* var. *ensifolius*]
< *Juncus filiformis* L. **[G,T]** 6900–7340′; JAC, YEL **[2]** str.
◄ *Juncus interior* Wieg. var. *interior* **[G,H]** 6700–8120′; JAC, YEL **[2]** bua, dis.
Juncus longistylis Torr. var. *longistylis* **[G,H]** 6816–7250′; JAC, PPH **[4]** mmc, scs, str.
Juncus mertensianus Bong. **[G,W,H]** 7160–10640′; PPH, TET, YEL **[11]** alt, mmm, sum, scs, str, tas.
Juncus nevadensis Wats. var. *nevadensis* **[G,W]** 6960–7020′; JAC, YEL **[2]** mmc, str, wet.
Juncus nodosus L. **[T]** 6500′; YEL **[1]** wet.
Juncus parryi Engelm. **[G,H]** 7995–11320′; PPH, TET **[14]** alt, mmc, sum, smc, tas.
Juncus regelii Buch. **[H]** 6930′; PPH **[1]** str.
Juncus saximontanus A. Nelson **[G,W,H,T]** 6491–7780′; JAC, PPH, TET, YEL **[16]** aqu, mmm, scs, str, wet. [*Juncus ensifolius* Wikstr. var. *montanus* (Engelm.) C.L. Hitchc.]
Juncus tweedyi Rydb. **[H,T]** 6460–7539′; PPH, YEL **[3]** str, wet.
◄> *Luzula glabrata* (Hoppe ex Rostk.) Desv. var. *hitchcockii* (Hamet-Ahti) Dorn **[G]** 7860–10600′; TET **[4]** mmc, tas.
► *Luzula multiflora* (Ehrh.) Lej. **[G,W]** 6920–7360′; JAC, YEL **[2]** mmm, mmc.
Luzula parviflora (Ehrh.) Desv. **[G,W,H,T]** 6960–10390′; JAC, PPH, TET, YEL **[17]** alt, mmm, mmc, sum, str, tas, wib.
Luzula piperi (Cov.) Jones **[G]** 10640–10800′; TET **[2]** alt, clf. [*Luzula wahlenbergii* Rupr.]
Luzula spicata (L.) DC. **[G]** 8000–11320′; TET **[12]** alt, clf, smc, str.

Juncaginaceae

Triglochin maritima L**.** **[G,W]** 6790–6905′; JAC, YEL **[3]** aqu, wet. [*Triglochin maritima* var. *elata* (Nutt.) A. Gray]
► *Triglochin palustris* L. **[W]** 6905′; YEL **[1]** wet.

Lamiaceae

Agastache urticifolia (Benth.) Kuntze var. *urticifolia* **[G,H]** 6750–7840′; JAC, PPH, TET **[6]** mm, mmc, mos, str.
Dracocephalum parviflorum Nutt. **[G]** 6560–6932′; JAC **[2]** dis, sps.
Mentha arvensis L. **[G,W,H,T]** 6333–7550′; JAC, TET, YEL **[15]** mmm, str, wet. [*Mentha arvensis* var *canadensis* (L.) Kuntze]
Prunella vulgaris L.ssp. *lanceolata* (Barton) Hulten **[G,W]** 6563–6905′; JAC, TET, YEL **[3]** str, wet. [*Prunella vulgaris*]
Scutellaria galericulata L. **[G,W,H,T]** 6491–7550′; JAC, PPH, YEL **[8]** mmm, str, wet.

Lemnaceae

► *Lemna gibba* L. **[W]** 6905′; YEL **[1]** aqu. *Lemna minuta* Kunth **[G,W]** 6905–7390′; JAC, YEL **[2]** aqu.
Lemna trisulca L. **[H]** 7440–8320′; PPH **[3]** aqu.
Lemna turionifera Landolt **[G,H]** 6563–8320′; JAC, PPH **[8]** aqu.

◄> *Spirodela polyrhiza* (L.) Schleid. **[G,H]** 7390–8320′; JAC, PPH **[4]** aqu.

Lentibulariaceae

Utricularia macrorhiza Leconte **[G,W,T]** 6460–6905′; JAC, YEL **[4]** aqu, wet.

< *Utricularia minor* L. **[W]** 6840–7155′; YEL **[2]** aqu, str, wet.

Liliaceae

Allium brevistylum Wats. **[G,H]** 6551–7390′: JAC, PPH, TET **[5]** mmc, sas, str.

Allium geyeri Wats. var. *tenerum* Jones **[G]** 6880′: JAC **[1]** mmm.

Allium schoenoprasum L. **[G,W,H]** 6850–9400′: JAC, PPH, TET, YEL **[7]** alt, mm, mmm, mmc, str, wib.

Calochortus nuttallii T. & G. **[G]** 6932′; JAC **[1]** sps.

Camassia quamash (Pursh) Greene ssp. *utahensis* Gould **[G,W]** 6820–7360′; JAC, YEL **[4]** mmm, mmc, wib.

Erythronium grandiflorum Pursh ssp. *grandiflorum* **[G,W,H]** 6920–9140′; PPH, TET, YEL **[4]** mmc, smc, str, wet.

Fritillaria atropupurea Nutt. **[G,H]** 6594–8640′; JAC, PPH, TET **[22]** asf, mm, mmc, sas, tas.

Fritillaria pudica (Pursh) Spreng. **[G,W,H]** 6551–9200′; JAC, PPH, TET **[21]** bua, dis, mm, mos, sas, sum.

Lloydia serotina (L.) Salisb. ex Rchb. var. *serotina* **[G]** 9320–9607′; TET **[2]** alt, clf, tas.

Maianthemum racemosum (L.) Link ssp. *amplexicaule* (Nutt.) LaFrankie **[G]** 6594–9200′; JAC, TET **[15]** mmm, mmc, sps.

Maianthemum stellatum (L.) Link **[G,H]** 6551–8100′; JAC, PPH, TET **[29]** asf, mm, mmm, mmc, sas, str, wib.

Prosartes trachycarpa S. Watson **[G]** 6686–7380′; JAC, TET **[8]** mmc, mos.

Streptopus amplexifolius (L.) DC. **[G,W,H,T]** 6460–8040′; JAC, PPH, TET, YEL **[11]** mmm, str.

Triantha occidentalis (S. Watson) Gates ssp. *montana* (C.L. Hitchc.) Packer **[G,W,T]** 6500–9240′; TET, YEL **[7]** str, wet. [*Tofieldia glutinosa* (Michx.) Pers. var. *montana* (C.L. Hitchc.) R. J. Davis]

> *Xerophyllum tenax* (Pursh) Nutt. **[G,W,T]** 7340–7860′; **[3]** PPH, TET, YEL mmc.

Zigadenus elegans Pursh **[G]** 6854–10795′; TET **[9]** alt, mmc, sps, str.

Zigadenus venenosus Wats. var. *gramineus* (Rydb.) Walsh ex Peck **[G]** 6560–8000′; JAC, TET **[5]** bua, sas, sps.

Limnanthaceae

Floerkea proserpinacoides Willd. **[G,H]** 6720–8320′; JAC, PPH, TET, YEL **[17]** bua, mm, mmm.

Linaceae

Linum lewisii Pursh var. *lewisii* **[G,H]** 6400–10795′; JAC, PPH, TET **[21]** alt, asf, mm, mmc, sas, sum, sps, str.

Loasaceae

Mentzelia dispersa Wats. **[H]** 7300′; PPH **[1]** mmc.

Malvaceae

Iliamna rivularis (Dougl. ex Hook.) Greene **[G,H]** 6560–7740′; JAC, PPH, TET **[4]** bua, mm, mmc, mos.

Menyanthaceae

Menyanthes trifoliata L. **[G,W,H,T]** 6460–7539′; JAC, PPH, YEL **[7]** mmm, str, wet.

Nymphaeaceae

Nuphar lutea(L.) Sm. ssp. *polysepala* (Engelm.) E. O. Beal **[G,W,H,T]** 6333–10250′; JAC, PPH, YEL **[12]** aqu, wet. [*Nuphar polysepala* Engelm.]

Onagraceae

Camissonia breviflora (T. & G.) Raven **[G]** 6845′: JAC **[1]** wet.

Camissonia subacaulis (Pursh) Raven **[G,W,H]** 6820–6900′; JAC, YEL **[4]** mmm.

Chamerion angustifolium (L.) Holub ssp. *angustifolium* **[G,H,T]** 7220–9320′; PPH, TET, YEL **[7]** mmc, scs.

Chamerion angustifolium (L.) Holub ssp. *circumvagum* (Mosquin) Hoch **[G,W,H]** 6960–10450′; JAC, PPH, TET, YEL **[11]** bua, mmc, str. [*Chamerion angustifolium* var. *canescens* (A. W. Wood) N. & P. Holmgren]

Chamerion latifolium (L.) Holub **[G,H]** 7250–10390′; JAC, PPH, TET **[7]** scs, str, tas. [*Epilobium latifolium* L.]

Circaea alpina L. ssp. *pacifica* (Aschers. & Magnus) P.H. Raven **[G]** 7159′; JAC **[1]** str.

Epilobium anagallidifolium Lam. **[G]** 8160–11320′; TET **[8]** alt, clf, sum, str, tas.

Epilobium brachycarpum Presl **[G,W,H]** 6760–7790′; JAC, PPH, TET, YEL **[12]** dis, mmc, scs, sps, str.

◄ *Epilobium ciliatum* Raf. ssp. *ciliatum* **[G,W,H,T]** 6500–7780′; JAC, PPH, TET, YEL **[20]** bua, mmm, mmc, str, wet.

Epilobium ciliatum Raf. ssp. *glandulosum* (Lehm.) Hoch & P.H. Raven **[G,W,H]** 6680–7680′; JAC, PPH, TET, YEL **[9]** mmm, scs, str, wet, wib.

◄ *Epilobium clavatum* Trel. **[G,H]** 7250–10795′; PPH, TET **[12]** alt, scs, sps, str, tas.

◄ *Epilobium halleanum* Hausskn. **[G,W,H]** 7160–10305′; PPH, TET, YEL **[9]** alt, scs, str.

◄ *Epilobium hornemannii* Rchb. ssp. *hornemannii* **[G,W,H]** 6790–8885′; JAC, PPH, TET, YEL **[12]** bua, mmm, mmc, str, wib.

Epilobium lactiflorum Hausskn. **[G]** 6750–7210′; JAC, TET **[3]** mmc, wet.

Epilobium leptophyllum Raf. **[W]** 6905′; YEL **[1]** str. [*Epilobium palustre* L. var. *gracile* (Farw.) Dorn] *Epilobium oregonense* Hausskn. [W] 6905′; YEL [1] str, wet.

Epilobium palustre L. **[T]** 7340′; YEL **[1]** mmc.

► *Epilobium saximontanum* Hausskn. **[G,W,H]** 6854–10100′; JAC, PPH, TET, YEL **[9]** bua, mm, mmm, mmc, smc, wib.

Epilobium suffruticosum Nutt. **[G,W,H]** 6810–8280′; JAC, PPH, YEL **[9]** dis, scs, sps.

► *Gayophytum decipiens* Lewis & Szweyk. **[G]** 6700′; JAC **[1]** sas.

Gayophytum diffusum T. & G. ssp. *diffusum* **[G]** 6750–7000′; JAC **[3]** sas, str, wib.

Gayophytum diffusum T. & G. ssp. *parviflorum* F.H. Lewis & Szweykowski **[G,W,H,T]** 6460–7860′; JAC, PPH, TET, YEL **[11]** bua, dis, mm, mos, sas, wet. [*Gayophytum diffusum* var. *strictipes* (Hook.) Dorn]

◄ *Gayophytum racemosum* T. & G. **[G]** 6700′; JAC **[1]** mmc.

◄ *Gayophytum ramosissimum* T. & G. **[G]** 6743′; JAC **[1]** mmc.

Oenothera cespitosa Nutt. ssp. *cespitosa* **[G,H]** 6865–8400′; JAC, PPH **[4]** sas, sps.

Oenothera flava (A. Nels.) Garrett **[G,H]** 6750–7000′; JAC, PPH **[2]** mm.

Oenothera villosa Thunb. ssp. *strigosa* (Rydb.) W. Dietr. & P.H. Raven **[G,W]** 6400–6880′; JAC, YEL **[3]** dis, str.

Orchidaceae

Calypso bulbosa (L.) Oakes var. *americana* (R. Br.) Luer **[G,W,H]** 6594–7080′; JAC, TET, YEL **[10]** mmc, str. [*Calypso bulbosa*]

Corallorrhiza maculata (Raf.) Raf. var. occidentalis (Lindl.) Ames **[G,H]** 6800–7960′; JAC, PPH, TET **[8]** bua, mm, mmc.

Corallorrhiza mertensiana Bong. **[G]** 6800–8285′; JAC, TET **[6]** bua, mm, mmc, sas.

Corallorrhiza striata Lindl. **[G]** 6760′; TET **[1]** mmc.

Corallorrhiza trifida Chat. **[G]** 7515′; TET **[1]** mmc.

Corallorrhiza wisteriana Conrad **[G]** 6594–8285′; JAC, TET **[3]** mmc.

Goodyera oblongifolia Raf. **[G]** 6852–7360′; JAC, TET **[3]** mmc.

Listera borealis Morong **[G]** 6980′; JAC **[1]** wet.

Listera caurina Piper **[G,T]** 6852–7340′; TET, YEL **[2]** mmc.

< *Listera convallarioides* (Sw.) Nutt. ex Elliott **[G]** 6854–6975′; TET **[2]** mmc, str.

Listera cordata (L.) R. Br. **[G,W]** 6854–9140′; JAC, TET, PPH **[9]** mmc.

Piperia unalascensis (Spreng.) Rydb. **[G]** 6938–7691′; JAC, TET **[3]** mm, mmc, sps.

Platanthera aquilonis Sheviak **[W]** 7155′; YEL **[1]** mmm.

Platanthera dilatata (Pursh) Lindl. ex Beck var. *dilatata* **[G,H,T]** 6680–8420′; JAC, PPH, TET, YEL **[11]** mmm, scs, str.

Platanthera dilatata (Pursh) Lindl. ex Beck var. *albiflora* (Cham.) Ledeb. **[G,H]** 6816–8400′; JAC, PPH, TET **[8]** mmm, mmc, str.

Platanthera huronensis (Nutt.) Lindl. **[G,H]** 6820–8975′; JAC, PPH, TET **[11]** mmm, scs, str.

Platanthera obtusata (Banks ex Pursh) Lindl. **[G]** 7390′; JAC **[1]** mmm.

◄ *Platanthera stricta* Lindl. **[G,W,H]** 6816–8680′; JAC, PPH, TET, YEL **[8]** mmm, str.

Spiranthes romanzoffiana Cham. **[G,W,H,T]** 6500–8320′; JAC, PPH, YEL **[10]** mm, mmc, str, wet.

Orobanchaceae

Orobanche fasciculata Nutt. **[G]** 6594–7367′; JAC **[5]** bua, sas, sps.

Orobanche uniflora L. **[G,H]** 6710–9240′; JAC, TET, YEL **[9]** bua, mm, sas, sps. [*Orobanche uniflora* var. *occidentalis* (Greene) Taylor & MacBryde]

Plantaginaceae

Plantago eriopoda Torr. **[H]** 6940–8320′; PPH **[3]** dis, mm, mmm.

●*Plantago major* L. **[G]** 6680–6900′; JAC **[6]** dis, mmm, str, wet, wib.

Plantago tweedyi A. Gray **[H]** 7250–7390′; PPH **[2]** scs.

Poaceae

Achnatherum hymenoides (Roem. & Schult.) Barkworth **[G,H]** 6400–7367′; JAC **[6]** sas, sps, str.

Achnatherum lettermanii (Vasey) Barkworth **[G,H]** 6595–9300′; JAC, PPH, TET **[10]** mm, mmm, sas, sps, sum.

Achnatherum nelsonii (Scribn.) Barkworth ssp. *nelsonii* **[G,H]** 6560–8000′; JAC, PPH, TET **[10]** bua, mm, mos, scs.

Achnatherum nelsonii (Scribn.) Barkworth ssp. *dorei* (Barkw. & Maze) Barkw. **[G,H]** 6940–8975′; JAC, PPH, TET **[8]** bua, mm, mmm, scs.

> *Achnatherum nevadense* (Johnson) Barkworth **[H]** 8120–8720′; YEL **[1]** bua.

Achnatherum occidentale (Thurb. ex Watson) Barkworth **[G,W,H]** 6900–8280′; JAC, PPH, YEL **[4]** bua, mmc, sas, sps.

● *Agropyron desertorum* (Fisch. ex Link) Schult. **[G]** 6400–6820′; JAC **[4]** dis, sas, sps. [*Agropyron cristatum* (L.) Gaertn. var. *desertorum* (Fisch. ex Link) Dorn]

►● *Agropyron fragile* (Roth) P. Candargy **[G]** 6560′; JAC **[1]** bua. [*Agropyron cristatum* (L.) Gaertn. var. *fragile* (Roth) Dorn]

Agrostis exarata Trin. **[G,W,H,T]** 6460–8360′; JAC, PPH, TET, YEL **[14]** mmm, mmc, scs, str, wib.

Agrostis humilis Vasey **[G,H]** 7860–10100′; PPH, TET **[10]** alt, mm, mmm, mmc, sum, smc. [Agrostis thurberiana Hitchc.]

Agrostis idahoensis Nash **[W,H]** 7120–8680′; PPH, YEL **[4]** mm, mmm.

►< *Agrostis mertensii* Trin. **[G]** 10800–11320′; TET **[2]** alt, tas.

> *Agrostis oregonensis* Vasey **[H]** 8360′; PPH **[1]** wet.

Agrostis scabra Willd. **[G,W,H,T]** 6491–11320′; JAC, PPH, TET, YEL **[23]** alt, mm, mmm, scs, tas, wet.

● *Agrostis stolonifera* L. **[G,W,T]** 6680–7340′; JAC, YEL **[8]** aqu, str.

Agrostis variabilis Rydb. **[G,W,H]** 6880–10640′; PPH, TET, YEL **[9]** alt, clf, mmm, scs, tas.

Alopecurus aequalis Sobol. var. *aequalis* **[G,W,H,T]** 6400–8360′; JAC, PPH, YEL **[11]** aqu, mmm, wet.

Alopecurus alpinus J. E. Sm. **[G,W]** 6845–7400′; JAC, YEL **[2]** aqu, dis. [*Alopecurus borealis* Trin.]

◄● *Alopecurus pratensis* L. **[G,H]** 6790–8320′; JAC, PPH **[7]** aqu, dis, mm, mmc.

►● *Arrhenatherum elatius* (L.) Beauv. ex J. & K. Presl var. *elatius* **[G]** 6790′; JAC **[2]** dis.

● *Bromus arvensis* L. **[G]** 6400–6938′; JAC **[3]** dis, sas, sps. [*Bromus japonicus* Thunb. ex J. A. Murray]

Bromus carinatus H. & A. **[G,W,H]** 6700–9060′; JAC, PPH, TET, YEL **[38]** bua, mm, mmc, sas, scs, sum.

Bromus ciliatus L. **[G,W,H]** 6680–8885′; JAC, PPH, TET **[21]** mm, mmm, mmc, scs, str.

● *Bromus inermis* Leyss. ssp. *inermis* **[G,W,H]** 6551–7580′; JAC, PPH **[8]** bua, dis, mm, mmm.

Bromus inermis Leyss. var. *pumpellianus* (Scribn.) C.L. Hitchc. **[G]** 6800–8000′; JAC, TET **[4]** mmc, wet, wib.

Bromus porteri (J.M. Coult) Nash **[G,H]** 6760–7390′; JAC, PPH, TET **[4]** mmc, sas, scs, wib. [*Bromus anomalus* Rupr. ex Fourn.]

● *Bromus racemosus* L. **[G]** 6750–7000′; JAC **[1]** mmc, mog. [*Bromus commutatus* Schrad.]

● *Bromus tectorum* L. **[G,H]** 6551–7160′; JAC **[13]** bua, dis, mmc, mm, sas, sps.

Bromus vulgaris (Hook.) Shear **[G]** 7090–7115′; TET **[2]** bua, str.

Calamagrostis canadensis (Michx.) Beauv. **[G,W,H,T]** 6460–10250′; JAC, PPH, TET, YEL **[29]** alt, aqu, bua, mm, mmm, mmc, sum, wib.

Calamagrostis koelerioides Vasey **[G]** 6852′; TET **[1]** mmc.

► *Calamagrostis montanensis* Scribn. ex Vasey **[G]** 7366′; TET **[1]** bua.

Calamagrostis purpurascens R. Br. var. *purpurascens* **[G,H]** 9740–10350′; TET **[6]** alt, sps.

Calamagrostis rubescens Buckl. **[G,W,H]** 6920–8360′; JAC, PPH, YEL **[4]** mmc.

Calamagrostis scopulorum Jones **[H]** 7740′; PPH **[1]** scs.

Calamagrostis stricta (Timm) Koeler ssp. *stricta* **[G,W,H,T]** 6460–7390′; JAC, PPH, YEL **[7]** aqu, bua, mmm, str, wet.

Calamagrostis stricta (Timm) Koeler ssp. *inexpansa* (A. Gray) C.W. Greene **[G,H]** 7120–8885′; PPH, TET **[2]** mmc. [*Calamagrostis inexpansa* A. Gray]

Cinna latifolia (Trev. ex Goepp.) Griseb. **[G,W,H]** 7230–7740′; PPH, TET, YEL **[5]** mmc, scs, str.

● *Dactylis glomerata* L. **[G,W,H]** 6400–6930′; JAC, PPH, YEL **[7]** dis, mm, mmm.

Danthonia californica Boland. **[G]** 6880′; JAC **[1]** mmm.

Danthonia intermedia Vasey **[G,W,H]** 6700–10305′; JAC, PPH, TET, YEL **[9]** alt, mm, mmc, sas, sum.

Danthonia unispicata (Thurb.) Munro ex Macoun **[G]** 6573–6970′; JAC **[8]** sas.

Deschampsia cespitosa (L.) Beauv. **[G,W,H]** 6770–11320′; JAC, PPH, TET, YEL **[33]** alt, aqu, mmm, sum, tas, wib.

Deschampsia elongata (Hook.) Munro **[G,H]** 7580–8320′; PPH, TET **[5]** dis, mm, mmm, scs, wib.

Dichanthelium acuminatum (Sw.) Gould & Clark var. *acuminatum* **[W]** 6840–6859′; YEL **[2]** str, wet.

► *Elymus alaskanus* (Scribn. & Merr.) A. Löve ssp. *latiglumis* (Scribn. & J. G. Sm.) A. Löve **[G]** 9060–10795′; TET **[4]** alt, mm, sps. [Not recognized by Dorn]

◄ *Elymus albicans* (Scribn. & Sm.) Löve **[G]** 6900′; JAC [1] sps. [*Elymus albicans* var. *griffithsii* (Scribn. & Sm. ex Piper) Dorn]

Elymus elymoides (Raf.) Swezey ssp. *elymoides* **[G,W,H]** 6700–7920′; JAC, PPH, TET, YEL **[10]** bua, mm, mmc, sas.

Elymus elymoides (Raf.) Swezey ssp. *brevifolius* (J. G. Sm.) Barkw. **[G,H]** 6400–8600′; JAC, PPH, TET **[5]** mmc, sps.

Elymus glaucus Buckl. ssp. *glaucus* **[G,W,H,T]** 6795–9400′; JAC, PPH, TET, YEL **[24]** alt, mm, mmm, mmc, str, sum.

Elymus lanceolatus (Scribn. & Sm.) Gould ssp. *lanceolatus* **[G,H]** 6560–7367′; JAC **[4]** bua, mmc, sas.

Elymus scribneri (Vasey) Jones **[G]** 10000–11320′; TET **[3]** alt, tas.

Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus* **[G,W,H]** 6760–10450′; JAC, PPH, TET, YEL **[40]** alt, dis, mm, mmc, scs, sps, sum, wib.

Festuca brachyphylla Schult. ex Schult. & Schult. ssp. *coloradensis* Frederiksen **[G]** 8878–10640′; TET **[7]** alt, mmm, tas.

Festuca idahoensis Elmer ssp. *idahoensis* **[G,H]** 6560–8400′; JAC, PPH **[8]** bua, mm, mmc.

◄ *Festuca minutiflora* Rydb. **[G]** 11320′; TET **[1]** alt, tas.

Festuca saximontana Rydb. var. *saximontana* **[G,W,H]** 6700–10350′; JAC, PPH, TET, YEL **[11]** alt, dis, mm, sas, tas.

Glyceria borealis (Nash) Batch. **[G,H,T]** 6515–7550′; JAC, PPH, YEL **[4]** aqu, mmm, wet.

Glyceria grandis Wats. **[G,W]** 6680–7390′; JAC, YEL **[6]** aqu, mmm, str, wet.

Glyceria striata (Lam.) Hitchc. **[G,W,H,T]** 6860–7780′; JAC, PPH **[13]** str, wet. [*Glyceria elata* (Nash ex Rydb.) Jones]

Hesperostipa comata (Trin. & Rupr.) Barkworth ssp. *comata* **[G]** 6900–7160′; JAC **[2]** sps.

Hesperostipa comata (Trin. & Rupr.) Barkworth ssp. *intermedia* (Scribn. & Tweedy) Barkw. **[G]** 6400–6900′; JAC **[4]** mmc, sas.

Hierochloë odorata (L.) Beauv. **[G,W,H]** 6880–8270′; PPH, TET, YEL **[5]** mm, mmm, str, wib.

Hordeum brachyantherum Nevski **[G,H]** 6770–7780′; JAC, PPH **[10]** mmm, scs, str, wib.

Hordeum jubatum L. **[G]** 6845′; JAC **[1]** dis.

Koeleria macrantha (Ledeb.) Schult. **[G,W,H]** 6550–9300′; JAC, PPH, TET, YEL **[23]** asf, bua, mm, mmc, sps.

Leucopoa kingii (Wats.) W. A. Weber **[G]** 7200–9530′; TET **[12]** alt, clf, mmc, sum, sps.

Melica bulbosa Geyer ex Porter & Coult. **[G,H]** 7300–8130′; JAC, PPH **[6]** mm, mmc.

Melica spectabilis Scribn. **[G,W,H]** 6551–8720′; JAC, PPH, TET, YEL **[41]** asf, bua, dis, mm, mmm, mmc, sas, sum.

► *Melica subulata* (Griseb.) Scribn. var. *pammelii* (Scribn.) C.L. Hitchc. **[G,H]** 6795–7960′; JAC, PPH, TET **[9]** bua, mm, mmc, str. [*Melica subulata*]

Muhlenbergia andina (Nutt.) Hitchc. **[G,W]** 6840–6905′; JAC, YEL **[3]** str.

Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi **[W]** 6859′; YEL **[1]** str.

Muhlenbergia filiformis (Thurb. ex Wats.) Rydb. **[G,W,H,T]** 6460–8320′; JAC, PPH, TET, YEL **[15]** dis, mm, mmm, str, wet.

► *Muhlenbergia mexicana* (L.) Trin. **[W]** 6840′; YEL **[1]** str, wet.

Muhlenbergia richardsonis (Trin.) Rydb. **[G,W,H,T]** 7250′; PPH **[1]** scs.

Nassella viridula (Trin.) Barkworth **[G]** 6700–6900′; JAC **[1]** sas.

Phalaris arundinacea L. **[G]** 6563–6980′; JAC **[4]** aqu, str.

Phleum alpinum L. **[G,H]** 7000–10305′; JAC, PPH, TET **[22]** alt, mmm, mmc, sum, wet, wib.

● *Phleum pratense* L. **[G,H]** 6597–8915′; JAC, PPH, TET **[17]** bua, dis, mmm, mmc, mos, sps, sas, wib.

Piptatherum exiguum (Thurb.) Dorn **[G,H]** 7560–9200′; PPH, TET **[3]** mmc, sps.

Poa abbreviata R. Br. ssp. *pattersonii* (Vasey) A. Löve & D. Löve & Kapoor **[G]** 8975–10795′; TET **[4]** alt, mm, sps. [*Poa pattersonii* Vasey]

Poa alpina L. **[G,H]** 6770–10390′; JAC, PPH, TET **[29]** alt, clf, scs, sum, tas, wib.

● *Poa annua* L. **[G]** 6680–8420′; JAC, TET **[4]** mmm, str.

● *Poa bulbosa* L. **[G]** 6520–6570′; JAC **[1]** dis.

● *Poa compressa* L. **[G]** 6400–6900′; JAC **[3]** dis, wet.

Poa cusickii Vasey ssp. *epilis* (Scribn.) W. A. Weber **[G,H]** 8915–10600′; PPH, TET **[7]** alt, clf, sum, tas.

Poa cusickii Vasey ssp. *pallida* Soreng **[G]** 9060–9800′; TET **[2]** sum, tas.

Poa fendleriana (Steud.) Vasey **[G,H]** 6758–10305′; JAC, PPH, TET **[15]** alt, mm, mmm, mmc, mos, sas, tas.

Poa leptocoma Trin. **[G,H]** 6790–10350′; JAC, PPH, TET **[7]** aqu, mm, mmm, mmc, tas.

Poa nemoralis L. ssp. *interior* (Rydb.) W.A. Weber **[G,H,T]** 6515–10040′; JAC, PPH, TET, YEL **[12]** alt, mmc, scs, sps, sum, tas, wib. [*Poa interior* Rydb.]

Poa palustris L. **[G,W,T]** 6400–7785′; JAC, PPH, TET, YEL **[16]** bua, mmm, mmc, str, wet.

● *Poa pratensis* L. **[G,W,H,T]** 6400–10795′; JAC, PPH, TET, YEL **[40]** bua, dis, mm, mmm, mmc, mos, sas, scs, sps, sum, wib.

Poa reflexa Vasey & Scribn. ex Vasey **[G,W,H]** 6980–10640′; JAC, PPH, TET, YEL **[23]** alt, aqu, mm, mmm, mmc, mos, scs, str.

Poa secunda Presl **[G,W,H]** 6520–11320′; JAC, PPH, TET, YEL **[57]** alt, bua, mm, mmm, mmc, mos, sas, sps, tas wet. [*Poa nevadensis* Vasey ex Scribn.] [*Poa secunda* varieties] [*Poa gracillima* Vasey]

Poa wheeleri Vasey **[G,W,H]** 6551–10295′; JAC, PPH, TET, YEL **[57]** alt, bua, mm, mmm, mmc, sas, smc, str.

Pseudoroegneria spicata (Pursh) A. Löve ssp. *spicata* **[G,H]** 6560–9300′; JAC, TET **[14]** alt, bua, mm, mmc, sas, sps. [*Elymus spicatus* (Pursh) Gould]

× *Pseudelymus ×saxicola* (Scrib. & J.G. Sm.) Barkworth & D.R. Dewey **[G]** 10480′; TET **[1]** alt. [*Elymus ×saxicolus*]

● *Schedonorus phoenix* (Scop.) Holub **[H]** 7255′; PPH **[1]** mm. [*Festuca arundinacea* Schreb.]

● *Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey **[G]** 7340′; TET **[1]** mm, mos. [*Elymus hispidus* (Opiz) Melderis var. *hispidus*]

Trisetum spicatum (L.) Richt. **[G,W,H]** 6780–11320′; JAC, PPH, TET, YEL **[37]** alt, mm, mmm, mmc, scs, str, tas.

Trisetum wolfii Vasey **[H]** 7300–8680′; PPH **[3]** mmm, str.

Vahlodea atropurpurea (Wahlenb.) Fr. ex Hartm. **[G,H]** 8680–10640′; PPH, TET **[5]** alt, clf, smc, str. [Deschampsia atropurpurea (Wahl.) Scheele]

Polemoniaceae

Collomia linearis Nutt. **[G,W,H]** 6400–9130′; JAC, PPH, TET, YEL **[43]** asf, bua, mm, mmm, mmc, mos, sas, scs, sum.

► *Collomia tenella* A. Gray **[G,H]** 7040–8640′; JAC, PPH, TET **[4]** mm, mos, sps.

Ipomopsis aggregata (Pursh) V. Grant var. *aggregata* **[G,H]** 6551–8880′; JAC, PPH, TET **[27]** bua, mm, mmc, sas, scs, sps, sum.

Lathrocasis tenerrima (A. Gray) L. A. Johnson **[G,H]** 6700–7440′; JAC, PPH **[4]** mmc, mos, sas.

Leptosiphon nuttallii (A. Gray) J.M. Porter & L. Johnson ssp. *nuttallii* **[G]** 8300–9635′; TET **[5]** mm, sps, tas.

Leptosiphon septentrionalis (Mason) J.M. Porter & L.A. Johnson **[G,H]** 6551–8500′; JAC, PPH, TET **[26]** bua, mm, mmm, mmc, sas.

Linanthus pungens (Torr.) J. M. Porter & L.A. Johnson **[G,H]** 6560–8320′; JAC **[9]** mmc, sas, sps.

Microsteris gracilis (Hook.) Greene var. *gracilis* **[G]** 6700′; JAC **[1]** sas.

Microsteris gracilis (Hook.) Greene var. *humilior* (Hook.) Cronq. **[G]** 6520–7000′; JAC **[6]** dis, sas, sps, str.

Phlox hoodii Richards. **[G,H]** 6597–8878′; JAC, TET **[5]** clf, sas, sps.

Phlox longifolia Nutt. ssp. *longifolia* **[G,H]** 6397–8640′; JAC, PPH **[11]** bua, mmc, sas.

Phlox multiflora A. Nels. **[G,W,H]** 6760–10795′; JAC, PPH, TET, YEL **[13]** alt, clf, mmm, sas, sps.

Phlox pulvinata (Wherry) Cronq. **[G]** 8500–9640′; TET **[2]** sps, sum.

Polemonium occidentale Greene ssp. *occidentale* **[G]** 7185′; TET **[1]** wib.

Polemonium pulcherrimum Hook. ssp. *pulcherrimum* **[G,H]** 6700–8400′; JAC, PPH **[3]** scs, sum.

Polemonium viscosum Nutt. **[G]** 8878–10600′; TET **[8]** alt, sps, tas.

Polygonaceae

Eriogonum brevicaule Nutt. var. *laxifolium* (T. & G.) Reveal **[H]** 10040′; TET **[1]** alt.

Eriogonum flavum Nutt. var. *piperi* (Greene) Jones **[H]** 8450′; PPH **[1]** mm.

Eriogonum ovalifolium Nutt. var. *purpureum* (Nutt.) Durand **[G]** 9300–10875′; TET **[6]** alt, tas.

Eriogonum umbellatum Torr. var. *umbellatum* **[G,H]** 6806–6865′; JAC **[2]** sas, sps.

Eriogonum umbellatum Torr. var. *majus* Hook. **[G,W,H]** 6551–10480′; JAC, PPH, TET, YEL **[44]** bua, dis, mmc

Oxyria digyna (L.) Hill **[G,H]** 7210–10800′; TET, YEL **[14]** alt, clf, tas.

Polygonum amphibium L. var. *stipulaceum* Coleman **[G,W,H,T]** 6400–7549′; JAC, PPH, YEL **[10]** aqu, wet.

Polygonum aviculare L. **[G]** 6680′; JAC **[1]** mmm.

Polygonum bistortoides Pursh **[G,H]** 6607–10795′; JAC, PPH, TET **[20]** alt, clf, mmm, mmc, sps, tas.

Polygonum douglasii Greene var. *douglasii* **[G,W,H,T]** 6400–8915′; JAC, PPH, TET, YEL **[26]** aqu, mm, mmm, mmc, sas, sps, str, wib.

Polygonum lapathifolium L. **[G]** 6845′; JAC **[1]** wet.

Polygonum minimum Wats. **[G]** 7360′; TET **[1]** sps.

Polygonum polygaloides Wall. ex Meisn ssp. *confertiflorum* (Nutt. ex Piper) J.C. Hickman **[G,H]** 6900–7980′; JAC, PPH **[3]** dis, wet. [*Polygonum kelloggii* Greene var. *confertiflorum* (Nutt. ex Piper) Dorn]

Polygonum polygaloides Wall. ex Meisn ssp. *kelloggii* (Greene) J.C. Hickman **[G,H]** 6700–8680′; JAC, PPH **[4]** dis, mmm. [*Polygonum kelloggii* Greene var. *kelloggii*]

Polygonum viviparum L. **[G]** 7185–10255′; TET **[5]** alt, clf, scs, wib.

● *Rumex acetosella* L. **[G]** 6551–7000′; JAC **[7]** sas, sps.

► *Rumex aquaticus* L. var. *fenestratus* (Greene) Dorn **[W]** 6810′; YEL **[1]** wet.

● *Rumex crispus* L. **[G,W,T]** 6400–6980′; JAC, YEL **[3]** aqu, str, wet.

Rumex maritimus L. **[G]** 6680–6975′; JAC **[3]** mmm, wet. [*Rumex maritimus* var. *fueginus* (Phil.) Dusen]

Rumex paucifolius Nutt. **[G,W,H]** 6397–10100′; JAC, PPH, TET, YEL **[26]** asf, bua, mm, mmm, sas, smc, wib.

Rumex salicifolius Weinm. var. *mexicanus* (Meisn.) C.L. Hitch. **[G]** 6400–6868′; JAC **[2]** str. [*Rumex salicifolius* var. *triangulivalvis* (Danser) C.L. Hitch.]

Portulacaceae

Cistanthe umbellata (Torr.) Hershkovitz var. *caudicifera* (A. Gray) Kartesz & Gandhi **[H]** 9590′; PPH **[1]** sum. [*Cistanthe umbellata*]

Claytonia lanceolata Pall. ex Pursh var. *lanceolata* **[G,W,H]** 6594–9640′; JAC, PPH, TET, YEL **[25]** dis, mm, mmm, mmc, sas, smc, sps, str.

Claytonia megarhiza (A. Gray) Parry ex Wats. var. *megarhiza* **[G]** 11320'; TET **[1]** alt.
Lewisia pygmaea (A. Gray) Robins. var. *pygmaea* **[G,H]** 6700–10305'; JAC, PPH, TET, YEL **[11]** alt, mm, sas, smc, sps, str.
Lewisia triphylla (Wats.) Robins. **[G,H]** 7000–9530'; PPH, TET **[7]** mm, mmc, sps, sum.
Montia chamissoi (Ledeb. ex Spreng.) Greene **[G,W]** 6850–7185'; JAC, TET, YEL **[4]** mmm, str, wib.

Potamogetonaceae
Potamogeton alpinus Balbis **[G,W,T]** 6680–7340'; JAC, JDR, YEL **[3]** aqu, mmm.
Potamogeton epihydrus Raf. **[T]** 6460'; YEL **[1]** aqu.
Potamogeton foliosus Raf. **[G,W]** 6820–6900'; JAC, YEL **[4]** aqu, str, wet.
Potamogeton natans L. **[T]** 7348'; YEL **[1]** wet.
Potamogeton richardsonii (Benn.) Rydb. **[G]** 6845–6935'; JAC **[2]** aqu.
Stuckenia pectinata (L.) Boerner **[G]** 6680'; JAC **[1]** aqu.

Primulaceae
Androsace filiformis Retz. **[G,W,H]** 7159–8320'; JAC, PPH, YEL **[7]** mmm, str, wib.
Androsace septentrionalis L. ssp. *subulifera* (A. Gray) G.T. Robbins **[G,W,H]** 6607–10600'; JAC, PPH, TET, YEL **[35]** alt, asf, bua, dis, mm, mmm, mmc, sas, sps.
Dodecatheon conjugens Greene ssp. *conjugens* **[G]** 6889–8000'; JAC, TET **[2]** sas, str.
Dodecatheon pulchellum (Raf.) Merr. ssp. *pulchellum* **[G,H]** 6790–10305'; JAC, PPH, TET **[11]** alt, mm, mmm, sps, smc, tas, wib.
Primula parryi A. Gray **[G]** 9607–10640'; TET **[6]** alt, clf, str, sum, tas.

Ranunculaceae
Aconitum columbianum Nutt. ssp. *columbianum* **[G,W,H]** 6900–10100'; JAC, PPH, TET, YEL **[21]** mmm, smc, str, wib.
Actaea rubra (Ait.) Willd. **[G,H]** 6800–7598'; JAC, TET **[14]** mmc, str.
Anemone multifida Poir. var. *multifida* **[G,H]** 6640–7200'; JAC, TET **[6]** asf, mmc, wib.
Anemone multifida Poir. var. *tetonensis* (Porter ex Britton) C.L. Hitchc. **[G,H]** 6760–10040'; JAC, TET **[13]** alt, sps, sum, tas. [*Anemone tetonensis* Porter ex Britt.]
Aquilegia coerulea James var. *coerulea* **[G,H]** 6800–10350'; JAC, PPH, TET **[17]** clf, mmc, sps, str, sum, tas.
Aquilegia flavescens Wats. var. *flavescens* **[G,H]** 6760–9590'; JAC, PPH, TET **[8]** mmc, str, tas.
►> *Aquilegia formosa* Fisch. ex DC. **[G]** 6800'; JAC **[1]** str.
Caltha leptosepala DC. ssp. *leptosepala* **[G,H]** 8270–10305'; PPH, TET **[5]** bua, mm, mmc, sum.
Clematis hirsutissima Pursh var. *hirsutissima* **[G,H]** 6806–9635'; JAC, TET, YEL **[11]** bua, mmm, mmc, sum, tas, sps.
Clematis occidentalis (Hornem.) DC. var. *grosseserrata* (Rydb.) J. Pringle **[G,H]** 6800–7440'; JAC, PPH, TET **[10]** mmc, str.
◄ *Delphinium bicolor* Nutt. **[G,H]** 6594–8310'; JAC, PPH, TET **[14]** mm, mmc, sas, sps.
× *Delphinium* ×*burkei* Greene **[G]** 6880'; JAC **[1]** mmm. [*Delphinium burkei*]
Delphinium glaucum Wats. **[G,H]** 7255–9140'; PPH, TET **[7]** mm, sum, wib.
Delphinium nuttallianum Pritz. ex Walp. **[G,W,H]** 6397–8300'; JAC, PPH, TET, YEL **[25]** asf, dis, mm, mmc, sas.
× *Delphinium* ×*occidentale* (Wats.) Wats. **[G,H]** 6930–7740'; PPH, TET **[3]** mm. [*Delphinium occidentale*]
Myosurus minimus L. **[H]** 7780'; PPH **[1]** mmm.
Ranunculus acriformis A. Gray var. *montanensis* (Rydb.) Benson **[G]** 6720–7080'; JAC **[5]** mmm, str, wib.
◄ *Ranunculus adoneus* A. Gray **[G]** 7598–10324'; TET **[6]** alt, mmc.
► *Ranunculus alismifolius* Geyer ex Benth. var. *alismifolius* **[G]** 6880'; JAC **[1]** mmm. [*Ranunculus alismifolius* var. *hartwegii* (Greene) Jeps.]
Ranunculus alismifolius Geyer ex Benth. var. *davisii* Benson **[H]** 8320'; PPH **[1]** mmm.
◄ *Ranunculus alismifolius* Geyer ex Benth. var. *montanus* Wats. **[G]** 7360'; JAC **[1]** mmm.
Ranunculus cymbalaria Pursh **[G]** 6563–6790'; JAC **[2]** aqu, mmm. [*Ranunculus cymbalaria* var. *cymbalaria*] [*Ranunculus cymbalaria* var. *saximontanus* Fern.]
Ranunculus eschscholtzii Schlecht. var. *eschscholtzii* **[G,H]** 7600–10305'; PPH, TET **[10]** alt, clf, mmc, str, wet.
Ranunculus eschscholtzii Schlecht. var. *trisectus* (Eastw.) Benson **[G,H]** 8915–10640'; PPH, TET **[9]** alt, mm, mmc, sum.
Ranunculus flammula L. var. *filiformis* (Michx.) Hook. **[G,W]** 6860–7160'; JAC, YEL **[4]** aqu, scs. [*Ranunculus flammula* var. *reptans* (L.) Meyer.]
Ranunculus glaberrimus Hook. var. *ellipticus* (Greene) Greene **[G,W]** 6900–8400'; JAC, TET, YEL **[4]** mm, mmm.
Ranunculus gmelinii DC. **[G,H]** 6980–7550'; JAC, TET **[2]** aqu, mmm.
◄ *Ranunculus hyperboreus* Rottb. **[W]** 7186'; YEL **[1]** wet.
Ranunculus inamoenus Greene var. *inamoenus* **[G,W,H]** 6790–8270'; JAC, PPH, TET, YEL **[10]** mm, mmm, str.
Ranunculus jovis A. Nels. **[G,W]** 7320–9740'; TET, YEL **[5]** dis, sps, smc.
Ranunculus macounii Britt. **[G,W]** 6563–6900'; JAC, YEL **[2]** wet.
Ranunculus orthorhynchus Hook. var. *orthorhynchus* **[W]** 6900'; YEL **[1]** mmc. [*Ranunculus orthorhynchus* var. *platyphyllus* A. Gray]
► *Ranunculus pensylvanicus* L. f. **[G,T]** 6400–6880'; JAC, YEL **[2]** mmm, wet.
► *Ranunculus pygmaeus* Wahlenb. var. *pygmaeus* **[G]** 10480'; TET **[1]** alt, clf.
►● *Ranunculus repens* L. **[G]** 6850'; JAC **[1]** mmm.
Ranunculus sceleratus L. var. *multifidus* Nutt. **[G]** 6845'; JAC **[1]** wet.
Ranunculus trichophyllus Chaix. var. *trichophyllus* **[G,W]** 6563–7200'; JAC, YEL **[3]** str, wet. [*Ranunculus aquatilis* L. var. *difusus* With.]
Ranunculus uncinatus D. Don ex G. Don var. *uncinatus* **[G,H]** 6850–8120'; JAC, PPH **[3]** mmm.
Ranunculus uncinatus D. Don ex G. Don var. *parviflorus* (Torr.) Benson **[G,H,T]** 6400–7785'; JAC, PPH, TET, YEL **[16]** mmm, str, wet. [*Ranunculus uncinatus*]
Thalictrum fendleri Engelm. ex A. Gray **[G,W,H]** 6780–8880'; JAC, PPH, TET **[14]** mmc, str, sum, wib.

Thalictrum occidentale A. Gray **[G,W,H]** 6816–8450′; JAC, PPH, TET, YEL **[9]** mm, mmc, str.

Thalictrum sparsiflorum Turcz. ex Fisch. & Mey. var. *saximontanum* Boivin **[T]** 6460–7340′; YEL **[2]** mmm, str.

◀ *Thalictrum venulosum* Trel. **[G,W]** 7280–7600′; TET, YEL **[2]** mm, mmc.

Trollius laxus Salisb. ssp. *albiflorus* (A. Gray) A. Löve & D. Löve & Kapoor **[G,W,H,T]** 6900–10100′; **[14]** mm, mmm, mmc, str, smc. [*Trollius albiflorus* (A. Gray) Rydb.]

Rhamnaceae

Ceanothus velutinus Dougl. ex Hook. **[G,H]** 6800–8280′; JAC, PPH, TET, YEL **[15]** mmc, mos, sps, str.

Rhamnus alnifolia L'Her. **[G]** 6680–6854′; JAC, TET **[2]** mmm, mmc, str.

Rosaceae

Amelanchier alnifolia (Nutt.) Nutt. ex Roem. var. *alnifolia* **[G,H]** 6551–8300′; JAC, PPH, TET **[18]** asf, bua, mm, mmc, mos, sas.

Amelanchier pumila (Torr. & A. Gray) Nutt. ex Roem. **[G,H,T]** 6479–8080′; JAC, PPH, TET, YEL **[15]** mm, mmc, sas, sps, wet. [*Amelanchier alnifolia* (Nutt.) Nutt. ex Roem. var. *pumila* (T. & G.) A. Nels.]

◀ *Amelanchier utahensis* Koehne **[G,H]** 6820–8000′; JAC, PPH, TET **[8]** mm, mmc, mos, sas, sps, wib.

Argentina anserina (L.) Rydb. **[G,W]** 6700–6900′; JAC, YEL **[3]** wet.

Comarum palustre L. **[W,H,T]** 6400–7550′; PPH, YEL **[13]** mmm, wet. [*Potentilla palustris* (L.) Scop.]

Dasiphora fruticosa (L.) Rydb. **[G,W,H]** 6400–9300′; JAC, PPH, TET, YEL **[24]** asf, mm, mmm, sas, sps, str, wib.

Dryas octopetala L. ssp. *hookeriana* (Juz.) Hulten **[G]** 10198–10795′; TET **[2]** alt.

Fragaria vesca L. **[G,H]** 6800–8000′; JAC, PPH, TET **[17]** mm, mmc.

Fragaria virginiana Duchesne **[G,W,H]** 6607–9635′; JAC, PPH, TET, YEL **[36]** asf, bua, mm, mmm, mmc, str.

► *Geum aleppicum* Jacq. **[G,W]** 6790–6859′; JAC, YEL **[2]** str.

Geum macrophyllum Willd. var. *perincisum* (Rydb.) Raup **[G,W,H,T]** 6680–8320′; **[31]** JAC, PPH, TET, YEL mmm, mmc, mog, str, wet.

Geum rossii (R. Br.) Ser. var. *turbinatum* (Rydb.) C.L. Hitchc. **[G]** 8980–10800′; TET **[4]** alt, sum, tas.

Geum triflorum Pursh var. *ciliatum* (Pursh) Fass. **[G,W,H]** 6560–7200′; JAC, TET **[15]** asf, bua, mm, mmm, sas.

Ivesia gordonii (Hook.) T. & G. **[G,H]** 9640–10040′; TET **[4]** alt, sps.

Petrophytum caespitosum (Nutt.) Rydb. var. *caespitosum* **[G,H]** 9320–10040′; TET **[2]** alt, clf. [*Petrophyton caespitosum*]

◀● *Potentilla argentea* L. **[G]** 6551–6880′; JAC **[3]** dis, sas.

◀ *Potentilla arguta* Pursh **[G,H]**6640–10450′; JAC, PPH, TET, YEL **[22]** mm, mmc, sas, scs, str, wet.

Potentilla brevifolia Nutt. ex T. & G. **[G]** 9590′; TET **[1]** alt.

Potentilla diversifolia Lehm. var. *diversifolia* **[G,W,H]** 6680–10795′; JAC, PPH, TET, YEL **[25]** alt, mm, mmm, mmc, smc, str.

Potentilla diversifolia Lehm. var. *perdissecta* (Rydb.) C.L. Hitchc. **[G]** 8775–10795′; TET **[6]** alt, tas.

Potentilla flabellifolia Hook. ex T. & G. **[G]** 9140–10305′; TET **[5]** alt, sum.

Potentilla glandulosa Lindl. ssp. *glabrata* (Rydb.) D.D. Keck **[H]** 7140′; PPH **[1]** mmc. [*Potentilla glandulosa* var. *intermedia* (Rydb.) C.L. Hitchc.]

Potentilla glandulosa Lindl. ssp. *pseudorupestris* (Rydb.) Keck **[G,H]** 6800–9485′; PPH, TET **[18]** mm, mmm, smc, sps, sum.

Potentilla gracilis Dougl. ex Hook. var. *brunnescens* (Rydb.) C.L. Hitchc. **[G,H]** 6720–8320′; JAC, PPH, TET **[9]** asf, mm, mmm, sas.

Potentilla gracilis Dougl. ex Hook. var. *fastigiata* (Nutt.) S. Watson **[G,W,H]** 6573–8120′; JAC, PPH, TET, YEL **[16]** dis, mm, mmc, sas, wib.

Potentilla gracilis Dougl. ex Hook. var. *flabelliformis* (Lehm.) Nutt. ex T. & G. **[G]** 6551–6960′; JAC **[3]** mmc, sas.

► *Potentilla hookeriana* Lehm. **[G]** 9385′; TET **[1]** alt, tas.

Potentilla norvegica L. **[G,W,T]** 6333–7366′; JAC, TET, YEL **[11]** dis, mmm, sas, wet.

◀ *Potentilla ovina* Macoun ex Macoun var. *ovina* **[G]** 9300–9607′; TET **[2]** alt, clf.

Potentilla pectinisecta Rydb. **[H]** 6940′; PPH **[1]** mm. [*Potentilla gracilis* Dougl. ex Hook. var. *elmeri* (Rydb.) Jeps.]

Potentilla pensylvanica L. **[G]** 6597′; JAC **[1]** sps.

Potentilla pulcherrima Lehm. **[G,H]** 6551–8885′; JAC, PPH, TET **[17]** bua, mm, mmc, sas, str, sum, wib. [*Potentilla gracilis* Dougl. ex Hook. var. *pulcherrima* (Lehm.) Fern.]

Potentilla rubricaulis Lehm. **[G]** 6597–8040′; JAC, TET **[2]** mog, sps.

Prunus virginiana L. var. *melanocarpa* (A. Nels.) Sarg. **[G,H]** 6597–8720′; JAC, PPH, TET, YEL **[27]** bua, dis, mm, mmm, mmc, mos, sas, sps.

Purshia tridentata (Pursh) DC. **[G,H]** 6397–6970′; JAC **[17]** dis, mmc, sas, sps.

► *Rosa acicularis* Lindl. ssp. *sayi* (Schwein.) W.H. Lewis **[G]** 6938′; JAC **[1]** sps. [*Rosa sayi* Schwein.]

Rosa nutkana Presl var. *hispida* Fern. **[G]** 6806′; JAC **[1]** mm, sps.

Rosa woodsii Lindl. **[G,H]** 6400–7691′; JAC, TET **[3]** mmc.

Rubus idaeus L. ssp. *strigosus* (Michx.) Focke **[G,H]** 6573–8885′; JAC, TET **[9]** mm, mmc, sps, tas.

Rubus parviflorus Nutt. var. *parviflorus* **[G]** 6573–7200′; JAC, TET **[8]** mos, str.

Sibbaldia procumbens L. **[G,H]** 8680–10795′; PPH, TET **[18]** alt, mm, smc, sum, tas.

Sorbus scopulina Greene var. *scopulina* **[G,H]** 6800–8000′; JAC, PPH, TET **[8]** mm, mmc, mos, sps.

Spiraea betulifolia Pall. var. *lucida* (Dougl. ex Hook.) C.L. Hitchc. **[G,W,H,T]** 6597–8885′; JAC, PPH, TET, YEL **[13]** mmc, sps, wet.

Spiraea splendens Baumann ex K. Koch **[G]** 6816–8985′; JAC, TET **[4]** asf, str.

Rubiaceae

Galium aparine L. **[G]** 6551–7934′; JAC, TET **[4]** sas, mm, mos.

Galium bifolium Wats. **[G,H]**6520–8915′; JAC, PPH, TET, YEL **[38]** mm, mmm, mmc, sas, sps, str.

Galium boreale L. **[G,W,H,T]** 6560–8140′; JAC, PPH, TET, YEL **[25]** bua, mmm, mmc, mos, wet.

Galium trifidum L. ssp. *trifidum* **[G,H,T]** 7340–8360'; PPH, TET, YEL **[6]** mmm, mmc, scs, wet.

Galium trifidum L. ssp. *subbiflorum* (Wieg.) Piper **[G,W,H,T]** 6400–8360'; JAC, PPH, YEL **[17]** mmm, wet, wib. [*Galium trifidum*]

Galium triflorum Michx. **[G,H,T]** 6460–7840'; JAC, PPH, TET, JDR; **[15]** mmm, mmc, wet.

> *Kelloggia galioides* Torr. [G] 7210'; TET [1] tas.

Salicaceae

Populus angustifolia James **[G,H]** 6400–8280'; JAC, PPH, TET **[21]** dis, mmc, sas, scs, str.

Populus balsamifera L. ssp. *balsamifera* **[G,H]** 6520–7934'; JAC, PPH, TET **[13]** mos, sps, str, wet.

► *Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray ex Hook) Brayshaw **[G]** 7109'; TET **[1]** tas. [*Populus balsamifera*]

Populus tremuloides Michx. **[G,H,T]** 6540–9189'; JAC, PPH, TET, YEL **[47]** asf, bua, mm, mmm, mmc, mos, sas, smc, sps, str.

Salix barclayi Anderss. **[H]** 7000–7580'; JAC, PPH **[3]** mmm, mos, wet.

Salix bebbiana Sarg. **[G,H]**6520–7180'; JAC **[7]** sas, sps, str, wet.

Salix boothii Dorn **[G,W,H,T]** 6551–10250'; JAC, PPH, TET, YEL **[19]** mm, mmm, scs, str, wet, wib.

◄ *Salix brachycarpa* Nutt. var. *brachycarpa* **[G]** 9635'; TET **[1]** sps, sum.

Salix cascadensis Ckll. **[G]** 9520–10800'; TET **[6]** alt, clf.

Salix drummondiana Barr. ex Hook. **[G,W,H,T]** 6515–9020'; JAC, PPH, TET, YEL **[8]** mmm, wet, wib.

Salix eastwoodiae Ckll. ex Heller **[G,H]**7600–9607'; PPH, TET **[10]** mm, mmm, smc, str, sum, wet.

Salix exigua Nutt. var. *exigua* **[H,T]** 6900–8120'; PPH, YEL **[2]** str.

Salix farriae Ball **[H]** 6900–8120'; JAC, PPH **[3]** mmc, mos.

►● *Salix fragilis* L. **[G]** 6520–6570'; JAC **[1]** dis

Salix geyeriana Anderss. **[G,T]** 6333–6816'; JAC, YEL **[6]** mmm, sas, str, wib.

Salix glauca L. var. *villosa* (D. Don ex Hook.) Anderss. **[G]** 6800–10305'; TET **[7]** alt, mm, sps, str, tas. [*Salix glauca* var. *villosa* Anderss.]

Salix lemmonii Bebb **[G,W]** 6551–7360'; JAC, YEL **[12]** mmm, str, wet.

Salix lucida Muhl. ssp. *caudata* (Nutt.) E. Murray **[G,T]** 6800–7340'; JAC, YEL **[2]** str. [*Salix lasiandra* Benth. var. *caudata* (Nutt.) Sudw.]

Salix melanopsis Nutt. **[G,H]** 6397–7620'; JAC, PPH **[6]** scs, str, wib.

Salix nivalis Hook. **[G]** 9320–10795'; TET **[6]** alt, clf, sps. [*Salix reticulata* L. var. *nana* Anderss.]

Salix petrophila Rydb. **[G]** 9240–10795'; TET **[6]** alt, clf, sum. [*Salix arctica* Pall. var. *petraea* (Anderss.) Bebb]

Salix planifolia Pursh ssp. *planifolia* **[W,T]** 6333–6527'; YEL **[5]** wet.

Salix scouleriana Barr. ex Hook. **[G,H,T]** 6500–8000'; JAC, YEL **[7]** mmc, sas, str, wet.

Salix tweedyi (Bebb ex Rose) Ball **[G]** 7670'; TET **[1]** mmc.

Salix wolfii Bebb **[G,W,H]** 6750–8985'; JAC, PPH, TET, YEL **[11]** mmm, str, wet, wib. [*Salix wolfii* var. *idahoensis* Ball] [*Salix wolfii* var. *wolfii*]

Santalaceae

Comandra umbellata (L.) Nutt. ssp. *pallida* (A. DC.) Piehl **[G,H]** 6400–7367'; JAC, TET **[11]** asf, bua, mos, sas, sps.

Saxifragaceae

Heuchera parvifolia Nutt. ex T. & G. **[G]** 6597–8915'; JAC, TET **[8]** bua, mmc, sps.

Lithophragma glabrum Nutt. **[G,W,H]** 6594–9530'; JAC, PPH, TET, YEL **[8]** mm, mmc, sps, sum.

Lithophragma parviflorum (Hook.) Nutt. ex T. & G. **[G,H]** 6720–8100'; JAC, PPH, TET **[18]** mm, mmm, mos, sps, str, sum.

► *Lithophragma tenellum* Nutt. **[G]** 6758–6820'; JAC **[1]** sps.

Mitella pentandra Hook. **[G,H]** 6816–9140'; JAC, PPH, TET **[10]** mmm, str.

Mitella stauropetala Piper var. *stauropetala* **[G,H]** 6760–8085'; JAC, PPH, TET **[7]** mmc, str, tas.

Parnassia fimbriata Konig var. *fimbriata* **[G,W,H]** 7090–10060'; PPH, TET, YEL **[10]** alt, clf, mmc, str, wet.

< *Parnassia kotzebuei* Cham. ex Spreng. **[G]** 9520'; TET **[1]** alt, clf.

Parnassia palustris L. var. *montanensis* (Fern. & Rydb.) C.L. Hitchc. **[G]** 6820'; JAC **[1]** str.

Parnassia palustris L. var. *parviflora* (DC.) B. Boivin **[W,H]**6880–7360'; PPH, YEL **[4]** scs, str. [*Parnassia parviflora* DC.]

Saxifraga bronchialis L. ssp. *austromontana* (Wieg.) Piper **[G]** 7210–10800'; TET **[14]** alt, clf, mmc, sps, str, tas.

► *Saxifraga caespitosa* L. ssp. *monticola* (Small) A.E. Porsild **[G]** 10198–10795'; TET **[2]** alt, tas. [*Saxifraga cespitosa*]

Saxifraga occidentalis Wats. **[G]** 7000–10305'; TET **[9]** alt, smc, sps, str.

Saxifraga odontoloma Piper **[G,W,H]** 6573–9800'; JAC, PPH, TET **[18]** alt, mmm, str, tas, wet.

Saxifraga oppositifolia L. **[G]** 10198–10795'; TET **[2]** alt.

Saxifraga rhomboidea Greene **[G]** 9740–10795'; TET **[2]** alt.

Saxifraga rivularis L. **[G]** 8980–10640'; TET **[6]** alt, clf, str, tas. [*Saxifraga rivularis* varieties]

Saxifraga subapetala E. Nels. **[G,H]** 6880–9200'; JAC, PPH, TET, YEL **[5]** mmm, str.

Telesonix heucheriformis Rydb. **[G,H]** 8878–10255'; TET **[9]** alt, clf, tas.

Scheuchzeriaceae

> *Scheuchzeria palustris* L. **[T]** 6491–6500'; YEL **[1]** wet.

Scrophulariaceae

Besseya wyomingensis (A. Nels.) Rydb. **[G]** 8160–8915'; TET **[2]** sps, sum.

Castilleja angustifolia (Nutt.) G. Don var. *dubia* A. Nels. **[G]** 7367'; JAC **[1]** sps.

Castilleja flava Wats. var. *flava* **[G,H]** 6400–9640'; JAC, TET **[6]** asf, sas, sps.

Castilleja linariifolia Benth. **[G,W,H]** 6400–8360'; JAC, PPH, TET, YEL **[12]** mmc, sas, scs, sps, wet.

Castilleja miniata Dougl. ex Hook. ssp. *miniata* **[G,W,H,T]** 6770–10640'; JAC, PPH, TET, YEL **[43]** alt, bua, mm, mmc, scs, str, tas, wib.

× *Castilleja miniata* Dougl. ex Hook. × *C. sulphurea* Rydb. [W] 6840–6905'; YEL [2] str, wet. [*Castilleja* ×*porterae* Ckll; not recognized by Dorn]

◀ *Castilleja pallescens* (A. Gray) Greenm. var. *pallescens* **[G]** 6560'; JAC **[1]** bua.

Castilleja pilosa (Wats.) Rydb. var. *longispica* (A. Nels.) N. Holmgren **[G]** 6400–7000'; JAC **[12]** sas, sps.

Castilleja pulchella Rydb. **[G]** 9600–10324'; TET **[5]** alt, sps, tas.

Castilleja rhexiifolia Rydb. **[G,H]**8400–10305'; PPH, TET **[3]** alt, str, sum. [*Castilleja rhexifolia* Rydb.]

Castilleja sulphurea Rydb. **[G,H]**7340–10600'; TET **[11]** mm, mos, smc, sum.

Collinsia parviflora Lindl. **[G,W,H]** 6397–8975'; JAC, PPH, TET, YEL **[41]** bua, dis, mm, mmm, mmc, sas, sps, sum.

▲● *Linaria dalmatica* (L.) Mill. ssp. *dalmatica* **[G]** 6400'; JAC **[1]** sas.

▲● *Linaria vulgaris* Mill. **[G,T,Y]** 6460–7366'; JAC, TET, YEL **[6]** bua, dis, mm, wet.

Mimulus guttatus DC. **[G,W,H]** 6563–8885'; JAC, PPH, TET, YEL **[16]** mmm, str, wet, wib.

Mimulus lewisii Pursh **[G,W,H]** 7120–10640'; PPH, TET, YEL **[14]** alt, mmm, scs, str, tas.

Mimulus moschatus Dougl. ex Lindl. var. *moschatus* **[G,W,H,T]** 6400–8360'; JAC, PPH, YEL **[15]** mmm, mmc, str, wet.

Mimulus tilingii Regel var. *tilingii* **[H,T]** 6333–8320'; PPH, YEL **[6]** mmm, scs, str, wet.

◀ *Mimulus washingtonensis* Gandog. **[G]** 7000–8953'; TET **[3]** clf, sps. [*Mimulus patulus* Penn.]

Orthocarpus luteus Nutt. **[G,W,H]** 6810–7580'; JAC, PPH, TET, YEL **[6]** dis, mm, mmm, wet, wib.

Orthocarpus tolmiei H. & A. **[G]** 8400–8885'; TET **[1]** mm.

Pedicularis bracteosa Benth. var. *paysoniana* (Penn.) Cronq. **[G,W,H]** 6750–9660'; JAC, PPH, TET, YEL **[25]** dis, mm, mmm, mmc, sas, smc.

Pedicularis contorta Benth. var. *contorta* **[G]** 10198–10795'; TET **[1]** alt.

Pedicularis groenlandica Retz. **[G,H]** 6854–10305'; JAC, PPH, TET **[23]** mm, mmm, scs, smc, str, sum, wib.

Pedicularis parryi A. Gray ssp. *purpurea* (Parry) G.D. Carr **[G]** 8980'; TET **[1]** alt.

Pedicularis racemosa Dougl. ex Benth. ssp. *alba* Penn. **[G,W,H,T]** 6460–10450'; JAC, PPH, TET, YEL **[19]** bua, mm, mmc, mos, smc, sum.

Penstemon attenuatus Dougl. ex Lindl. var. *pseudoprocerus* (Rydb.) Cronq. **[G,H]** 7210–10600'; PPH, TET **[11]** alt, mm, mmc, smc, sps, sum, tas.

Penstemon cyananthus Hook. **[G]** 7691–9300'; TET **[4]** clf, sum, sps.

Penstemon cyaneus Penn. **[G,H]** 7200–8400'; JAC, PPH, TET **[8]** mm, mmc, mos, sps.

Penstemon deustus Dougl. ex Lindl. var. *deustus* **[G]** 6806–9200'; JAC, TET **[4]** mos, sps, tas.

Penstemon montanus Greene var. *montanus* **[G,H]** 8878–10000'; PPH, TET **[6]** alt, sps, tas.

Penstemon procerus Dougl. ex Grah. var. *procerus* **[G,H]** 6400–8270'; JAC, PPH, TET **[11]** asf, mm, mmm, sas, scs.

Penstemon radicosus A. Nels. **[G,H]** 6560–7367'; JAC **[5]** bua, mmc, sps.

Penstemon subglaber Rydb. **[G]** 6400–6938'; JAC **[3]** sps.

Penstemon whippleanus A. Gray **[G,H]** 6770–10350'; JAC, PPH, TET **[10]** mmm, mmc, scs, smc, sps, sum, tas.

Scrophularia lanceolata Pursh **[G]** 6760–8500'; TET **[5]** mmc, mos, tas.

● *Verbascum thapsus* L. **[G,W]** 6790–6840'; JAC, YEL **[2]** dis.

Veronica americana Schwein. ex Benth. **[G,W,H,T]** 6460–10100'; JAC, PPH, TET, YEL **[20]** dis, mmm, smc, str, wib.

Veronica anagallis-aquatica L. **[G]** 6680'; JAC **[1]** str.

◀● *Veronica biloba* L. **[G,H]** 6640–8720'; JAC, PPH **[5]** dis, sps.

◀● *Veronica officinalis* L. **[G]** 6760'; JAC **[1]** dis.

Veronica peregrina L. ssp. *xalapensis* (H.B.K.) Pennell **[G]** 6700–6900'; JAC **[2]** dis, sas.

Veronica scutellata L. **[T]** 6400–6527'; YEL **[2]** wet.

Veronica serpyllifolia L. ssp. *humifusa* (Dicks.) Syme **[G,H]** 6700–8680'; JAC, PPH, TET, YEL **[11]** mmm, mmc, sas, str, wet, wib.

Veronica wormskjoldii R. & S. **[G,W,H]** 7580–10640'; PPH, TET, YEL **[17]** alt, clf, mmm, str, wet.

Sparganiaceae

Sparganium angustifolium Michx. **[G,W,H,T]** 6500–8065'; JAC, PPH, YEL **[8]** aqu, str, wet.

● *Sparganium emersum* Rehm. **[G,T]** 6400–6980'; JAC, YEL **[4]** aqu.

Typhaceae

Typha latifolia L. **[W]** 6810'; YEL **[1]** wet.

Urticaceae

Urtica dioica L. ssp. *gracilis* (Aiton.) Seland. **[G,H]** 6520–7350'; JAC, TET **[10]** mmc, mos, str. [*Urtica dioica* var. *procera* (Muhl. ex Willd.) Wedd.]

Valerianaceae

Valeriana acutiloba Rydb. var. *pubicarpa* (Rydb.) Cronq. **[G]** 9300'; TET **[1]** clf, sps.

Valeriana dioica L. var. *sylvatica* Wats. **[H]** 7560'; PPH **[1]** mmm, str.

Valeriana edulis Nutt. ex T. & G. var. *edulis* **[G,H]** 6720–9300'; JAC, PPH **[11]** mmm, mm, sps, wib.

Valeriana occidentalis Heller **[G,W,H]** 6520–9140'; JAC, PPH, TET, YEL **[41]** asf, bua, mm, mmm, mmc, mos, sas.

Verbenaceae

Verbena bracteata Cav. ex Lag. & Rodr. **[G]** 6700–6900'; JAC **[4]** dis, sas, wet.

Violaceae

Viola adunca Sm. **[G,W,H]** 6640–8100'; JAC, PPH, TET, YEL **[21]** asf, bua, mm, mmm, mmc.

Viola macloskeyi Lloyd ssp. *pallens* (Banks ex Ging.) M.S. Baker **[G,H,T]** 6460–8975'; JAC, PPH, TET, YEL **[10]** mm, mmm, str, wet.

Viola nephrophylla Greene **[G,H]** 7560–8400'; PPH, TET **[2]** clf, str, wet.

Viola orbiculata Geyer ex Holz. **[G,H]** 6760–8040'; PPH, TET **[2]** mm, str.

Viola palustris L. **[G,H]** 7360–9140'; JAC, PPH, TET **[7]** mmm, smc, str.

Viola praemorsa Dougl. ex Lindl. ssp. linguifolia (Nutt.) M.S. Baker & J.C. Clausen ex M. Peck **[G,W,H]** 6720–8975'; JAC, PPH, TET, YEL **[20]** bua, dis, mm, mmm, mmc, mos, sas, smc, str. [*Viola praemorsa* var. *altior* Blank.]

Viola purpurea Kellogg ssp. *venosa* (Wats.) M.S. Baker & J.C. Clausen **[G,H]** 6790–9635'; JAC, PPH, TET **[19]** mm, sas, smc, sps, sum.

> *Viola renifolia* A. Gray **[G]** 6980–7080'; JAC [1] wet. [*Viola renifolia* var. *brainerdii* (Greene) Fern.]

◀ *Viola vallicola* A. Nels. **[G,H]** 6594–9660'; JAC, PPH, TET **[8]** mm, mmc, sps, wet.

Viscaceae

Arceuthobium americanum Nutt. ex Engelm. **[G,W,T]** 6460–7040'; JAC, YEL **[7]** mmc.

Zannichelliaceae

Zannichellia palustris L. **[W]** 6820'; YEL **[4]** aqu.

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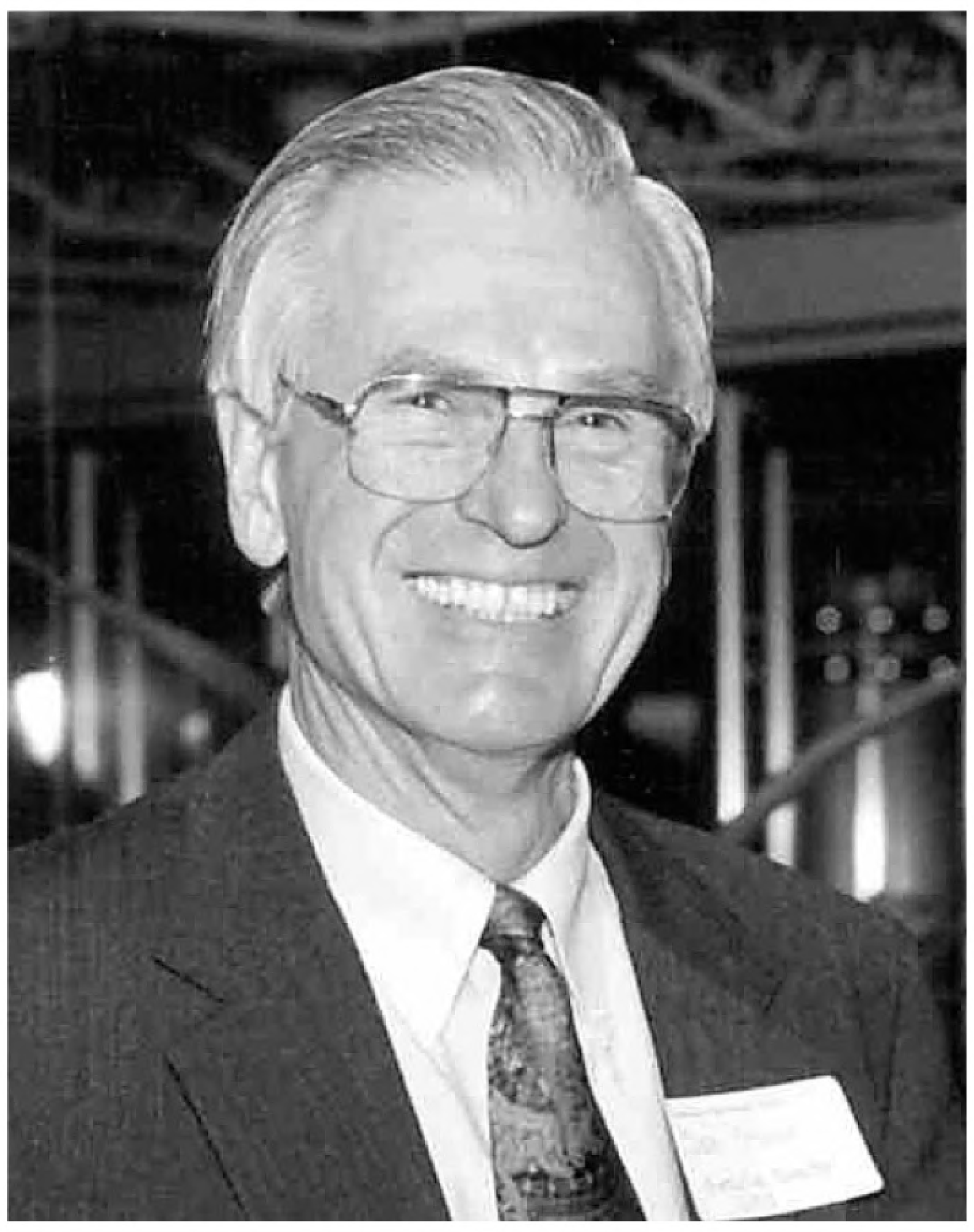

DONALD E. STONE
10 December 1930–4 March 2011

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Donald Eugene Stone died from a short bout with cancer on Friday, March 4, 2011 in Durham, North Carolina. Don was born on December 10, 1930 and grew up in Eureka, California. He took his undergraduate work at Humboldt State College and the University of California at Berkeley, graduating in 1952. He remained at Berkeley and was awarded his Ph.D. in Botany in 1957. Subsequently, he taught as a Lecturer and Assistant Professor at Tulane University for six years. In 1963, he joined the Botany Department at Duke University and taught at Duke for the remainder of his career. In 1969–70, Don took a one-year leave of absence to serve as the Associate Program Director in Systematic Biology at NSF where he was in charge of all plant research proposals. In 1976, while teaching as full professor at Duke, he began shepherding the Organization for Tropical Studies (OTS) as its Executive Director. During his tenure with OTS, Don expanded the consortium from twenty to more than 55 universities, museums, and research institutions. He enhanced the Organization's field-based graduate courses and created an on-the-ground training program for policy-makers. Most importantly, he strengthened OTS's three biological field stations in Costa Rica, La Selva, Las Cruces, and Palo Verde, as major research centers, and, in particular, established the La Selva station as one of the most important sites in the world for research in tropical biology. In the early 1980s, under Don's guidance, OTS took a leadership role, along with the John D. and Catherine T. MacArthur Foundation, the World Wildlife Fund, and The Nature Conservancy, in establishing a protected, 47,000–hectare, forested corridor from the Braulio Carrillo National Park, located in the central highlands of Costa Rica, to La Selva, more than 35 miles away in the Caribbean lowlands. As result of these efforts, in 1985 OTS was the first organization to be awarded the John and Alice Tyler Prize for Environmental Achievement. When Don retired from OTS in 1996, he served as the chair of the Botany Department at Duke for three years. In 2000, he joined the OTS Board of Visitors, which he formed in 1992, and from 2003–2005 he served in a volunteer capacity as OTS's Interim Executive Director during an 18–month search for the current CEO. In 1988 Don received

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the Distinguished Scientist Award from the American Institute of Biological Sciences; in 1993 he was recognized as an Honorary Fellow from the Association of Tropical Biology and Conservation; and in 2006 he was given the Centennial Award by the Botanical Society of America for his exemplary service to the plant sciences. Don's own research interest centered on the systematic and evolution of temperate and tropical plants, using biochemistry, cytotaxonomy, comparative anatomy and comparative morphology in the walnut family (Juglandaceae), and pollen development in the ginger family (Zingiberales). In addition to more than 60+ scientific papers and other publications, he authored or co-authored, he contributed Juglandaceae to the floras of Mesoamerica, Nicaragua, Costa Rica, and China as well as *Juglans* and *Carya* to the Flora of North America. Memorial contributions may be sent to OTS, Box 90633, Durham, NC 27708–0633.

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Stone, D.E. 2001. Juglandaceae. In: Stevens, W.D., et al., eds. Flora de Nicaragua. Monogr. Syst. Bot., Missouri Bot. Gard. 85(2):1160–1163.

Stone, D.E., S.-H. Oh, E.A. Tripp, L.E. Rios G, and P.S. Manos. 2009. Natural history, distribution, phylogenetic relationships, and conservation of Central American black walnuts (*Juglans* sect. *Rhysocaryon*). J. Torrey Bot. Soc. 136:1–25.

Manos, P.S., P.S. Soltis, D.E. Soltis, S.R. Manchester, S.-H. Oh, C.D. Bell, D.L. Dilcher, and D.E. Stone. 2007. Phylogeny of extant and extinct Juglandaceae inferred from the integration of molecular and morphological data sets. Syst. Biol. 56:1–19.

BOOKS RECEIVED | BOOK NOTICES

John Leslie Dowe. 2010. **Australian Palms: Biogeography, Ecology, and Systematics.** (ISBN 978-0643096158, pbk.). CSIRO Publishing, 150 Oxford Street (P.O. Box 1139), Collingwood VIC 3066, AUSTRALIA. (**Orders:** www.publish.csiro.au/pid/6164.htm; publishing-sales@csiro.au). AU140.00, 290 pp., b/w and color photos, 10¾" × 8¼".

From the Publisher: Australian Palms offers an updated and thorough systematic and taxonomic treatment of the Australian palm flora, covering 60 species in 21 genera. Of these, 54 species occur in continental Australia and six species on the off-shore territories of Lord Howe Island, Norfolk Island, and Christmas Island.

Sara Oldfield. 2010. **Botanic Gardens: Modern-Day Arks.** (ISBN 978-0-262-01516-5, hbk.). The MIT Press, 55 Hayward Street, Cambridge, Massachusetts 02142-1493, U.S.A. (**Orders:** mitpress.mit.edu/catalog/item/default.asp?ttype=2&tid=12399; special_sales@mitpress.mikt.edu). $29.95, 240 pp., 200 color photos, 10½" × 8½".

From the Publisher: All life depends on plants, but we often take them for granted in our everyday lives. It is easy to ignore the fact that we are facing a crisis: scientists estimate that one third of all flowering plant species are threatened with extinction. This lavishly illustrated volume considers the essential conservation role of botanic gardens, telling the story of how a global network is working to save our botanical heritage. Chapters feature gardens from countries around the world, including the United Kingdom, the United States, Australia, Germany, Turkey, Uganda, South Africa, Mexico, Brazil, and China.

Juliet C. Stromberg and Barbara Tellman, eds. 2009. **Ecology and Conservation of the San Pedro River.** (ISBN 978-0-8165-2752-6, hbk.). The University of Arizona Press, 355 S. Euclid Ave., Suite 103, Tucson, Arizona 85719, U.S.A. (**Orders:** www.uapress.arizona.edu/Books/bid2087.htm; 800-426-3797). $85.00, 529 pp., 7" × 10".

From the Publisher: This book provides an extensive knowledge base on all aspects of the San Pedro, from flora and fauna to hydrology and human use to preservation. It describes the ecological patterns and processes of this aridland river and explores both the ongoing science-driven efforts by nonprofit groups and government agencies to sustain and restore its riparian ecosystems and the science that supports these management decisions.

Klaus Mehltreter, Lawrence R. Walker, and Joanne M. Sharpe, eds. 2010. **Fern Ecology.** (ISBN 978-0-521-89940-6, hbk.; 978-0-521-72820-1, pbk.). Cambridge University Press, The Edinburgh Building, Cambridge CB2, 8RU, UK. (**Orders:** www.cambridge.org; www.cambridge.org/aus/catalogue/catalogue.asp?isbn=9780521728201&ss=fro). AUD$99.95, 460 pp., 93 b/w illus., 14 color illus., 32 tables, 9¾" × 6¾".

From the Publisher: Ferns are an integral part of the world's flora, appreciated for their beauty as ornamentals, problematic as invaders, and endangered by human interference. They often dominate forest understories but also colonize open areas, invade waterways, and survive in nutrient-poor wastelands and eroded pastures. This is the first comprehensive summary of fern ecology, with worldwide examples from Siberia to Hawaii. Topics include a brief history of the ecological study of ferns, their biogeography and population dynamics, their role in ecosystem nutrient cycles and adaptations to xeric environments, and their responses to disturbance and interactions with other organisms. Fully illustrated concepts provide a framework for students and professionals in ecology, conservation, and land management, and a wealth of information for anyone interested in ferns.

Walter Kingsley Taylor. 2009. **A Guide to Florida Grasses.** (ISBN 978-0-8130-3319-8, flexbound with flaps). University Press of Florida, 15 Northwest 25th Street, Gainesville, Florida 32611-2079, U.S.A. (**Orders:** www.upf.com; www.upf.com/book.asp?id=TAYLO004). $49.95, 361 pp., illustrated, 6" × 9".

From the Publisher: A Guide to Florida Grasses offers an introduction to this vital and frequently neglected plant family. This richly illustrated reference includes complete details pertaining to the identification, structure, distribution, and uses of more than 200 of the most common grasses found in Florida and nearby states.

With over 500 color images—some picturing species that have never been described with a published image—correctly identifying and selecting members of this important plant family has never been easier. Environmentalists, hikers, and nature lovers can take this

book into the field or enjoy it at home. *A Guide to Florida Grasses* will be accessible and invaluable to professional botanists, commercial landscapers, homeowners, and plant enthusiasts alike.

Patricia A. Harding. 2008. **Huntleyas and Related Orchids.** (ISBN 978-0-88192-884-6, hbk.). Timber Press, The Haseltine Building, 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com/books/huntleyas_related_orchids/harding/9780881928846; www.timberpress.com). $39.95, 260 pp., 150 color photos, 5 line drawings, 7⅜" × 10⅜".

From the Publisher: Revered by avid orchid collectors for its delightful, star-shaped flowers, *Huntleya* is a small group of orchids found low in the forest. Besides their striking colors—from deep blue to waxy red, royal purple to almost black—flowers of this group are known for their distinctive shapes, patterns, and textures. As appealing as these lovely tropical orchids are, their identification has been confused since the first species was described in the mid-1800s. Recent DNA studies have led to a clearer understanding of relationships and, as a result of this clarity, it is now possible to sort out the taxonomic problems and identify the characteristics that set species apart. In this first book devoted to the *Huntleya* alliance, author Patricia Harding presents evidence from the scientific literature, other growers, and her own experience that will enable orchidists everywhere to identify their plants and grow them successfully.

Alexander Krings. 2010. **Manual of the Vascular Flora of Nags Head Woods, Outer Banks, North Carolina.** (ISBN 978-0-89327-500-6, hbk.). Memoirs of the New York Botanical Garden, Volume 103 (ISSN 0077-8931). The New York Botanical Garden Press, 200th Street & Southern Boulevard, Bronx, New York 10458-5126, U.S.A. (**Orders:** www.nybgshop.org/Manual-of-the-Vascular-Flora-of-Nags-Head-Woods-Outer-Banks-North-Carolina-p-21584.html; Customer Service 718-817-8869). $62.00, 260 pp., illustrated, 7½" × 10½".

From the Publisher: "The Nags Head Woods complex (Outer Banks, Dare County, North Carolina) hosts the best remaining example of exceedingly rare, mid-Atlantic maritime deciduous forest and also includes an extensive system of open dunes, evergreen forest, interdunal ponds, swamps, and marshes. Over 550 plant species in 122 families have been reported from the site, constituting nearly three-quarters of the known Outer Banks flora. This manual was developed based on field and herbarium study and seeks to document the rich flora of Nags Head Woods. Keys, descriptions, and illustrations, as well as notes on phenology, habitat, and the broader distribution of included taxa on the Outer Banks, are provided. Relevant herbarium specimens known to the author from the main depositories of Outer Banks collections, as well as important literature reports, are cited after the species descriptions."

This is a very nice flora that every botanist in the US should have in their library.

Lane Greer and John M. Dole. 2009. **Woody Cut Stems for Growers and Florists: How to Produce and Use Branches for Flowers, Fruit, and Foliage.** (ISBN 978-0-88192-892-1, hbk.). Timber Press, The Haseltine Building, 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com). $39.95, 512 pp., 137 color photos, 9 line drawings, 6" × 9".

From the Publisher: Woody cut stems are the focus of a burgeoning, worldwide business. Until now, professional growers have lacked a resource that addresses how to choose, cultivate, and handle these popular plants. *Woody Cut Stems for Growers and Florists* fills this gap. It includes detailed information on 100 woody genera used for cut stems, extensive production guidelines, and explanations of techniques such as pruning, coppicing, and forcing. Rounding out the book are useful charts and tables that list species according to characteristics such as color, season of bloom, use, and fragrance. Growers who have been eager to add woody cut stems to the products they produce will find all the information they need to expand their business in an exciting and profitable new direction.

Matthew A. Jenks and Andrew J. Wood. 2007. **Plant Desiccation Tolerance.** (ISBN 978-0-8138-1263-2, hbk.). Blackwell Publishing Professional, 2121 State Avenue, Ames, Iowa 50014, U.S.A. (**Orders:** www.blackwellprofessional.com; www.wiley.com/WileyCDA/WileyTitle/productCd-0813812631.html; 1-800-0862-6657). $219.95, 340 pp., 7" × 10".

From the Publisher: Plant desiccation tolerance is of great basic and applied scientific interest. Understanding plant responses and adaptations to severe desiccation is key to applying desiccation tolerance research to the improvement of economically important crops. *Plant Desiccation Tolerance* brings together a field of international researchers to provide a current review of the advances in plant desiccation tolerance research. The book is broken up into three sections: Vegetative Desiccation Tolerance; Desiccation Tolerance of Pollen, Spores, and Seeds; and Applications of Desiccation Tolerance Research. Completely up-to-date and written by leading desiccation experts, *Plant Desiccation Tolerance* will be of great interest to plant researchers and plant and crop science professionals.

Tod F. Stuessy. 2009. **Plant Taxonomy: The Systematic Evaluation of Comparative Data, Second Edition.** (ISBN 978-0-231-14712-5, hbk.). Columbia University Press, 61 West 62nd Street, New York, New York 10023, U.S.A. (**Orders:** cup.columbia.edu/book/978-0-231-14712-5/plant-taxonomy). $99.50, 568 pp., 60 halftones, 16 color illus., 105 line drawings, 16 tables, 8½" × 11".

From the Publisher: The field of plant taxonomy has transformed rapidly over the past fifteen years, especially with regard to improvements in cladistic analysis and the use of new molecular data. The second edition of this popular resource reflects these far-reaching and dramatic developments with more than 3,000 new references and many new figures. Synthesizing current research and trends, *Plant Taxonomy* now provides the most up-to-date overview in relation to monographic, biodiversity, and evolutionary studies, and continues to be an essential resource for students and scholars.

This book is also available in eformat (ISBN 978-0-231-51864-2).

Nancy C. Garwood. Illustrated by Margaret Tebbs. 2009. **Seedlings of Barro Colorado Island and the Neotropics.** (ISBN 978-0-8014-4753-2, hbk.). Natural History Museum, London, in association with Cornell University Press, Sage House, 512 East State Street, Ithaca, New York 14850, U.S.A. (**Orders:** www.cornellpress.cornell.edu). $99.95, 645 pp., 255 plates, 8" × 11".

From the Publisher: "Few field guides exist to the plants of the American tropics. Guides to the juvenile stages of plants are rare for any part of the world. A guide to identification of tropical seedlings, from trees to herbs, is something to be treasured. Nancy Garwood's lifelong devotion to the study of the ecology and taxonomy of seedlings, combined with Margaret Tebbs's superb illustrations, has given us this first comprehensive guide to juvenile plants in the American tropics."—from the Foreword by Robin B. Foster

Stewart McPherson. Edited by Alastair Robinson and Andreas Flesichmann. 2009. **Pitcher Plants of the World, Volume 1 and Volume 2.** (ISBN 978-0-955918-2-3 [vol. 1]; 978-0-955918-3-0 [vol. 2], hbk.). Redfern Natural History Publications, Poole, Dorset, England, UK. (**Orders:** www.redfernnaturalhistory.com/books/name/_pitcher_plants_of_the_old_world_volume_one_-_hardback). £34.99 (vol. 1), £34.99 (vol. 2), 631 pp. (vol. 1), 766 pp. (vol. 2), 751 images, 6" × 9".

From the Publisher: Pitcher plants include the largest and most spectacular of all carnivorous plants. So-called because they produce highly specialised foliage that takes the form of hollow, water-filled "pitchers," these extraordinary plants lure and prey upon arthropods and other small animals. The pitcher plants of the Old World also trap the largest prey of all carnivorous plants, including on rare occasions, vertebrates as large as frogs, mice and even rats. This two-volume work examines both genera of Old World pitcher plants (*Nepenthes* and *Cephalotus*) and documents the ecology and natural diversity of every known species for the first time and in unparalleled detail...

Pitcher Plants of the Old World Volume One consists of the following chapters; Introduction, Carnivorous Plants of the World, The Pitcher Plants of the Old World, The Evolution of the Pitcher Plants of the Old World, Trapping Processes, Infauna, *Nepenthes* of Borneo and *Nepenthes* of Peninsular Malaysia and Indochina.

Pitcher Plants of the Old World Volume Two comprises *Nepenthes* of the Philippines, *Nepenthes* of Sumatra and Java, *Nepenthes* of Sulawesi, *Nepenthes* of New Guinea and the Maluku Islands, *Nepenthes* of the Outlying Areas, *Nepenthes* Hybrids, *Cephalotus follicularis*, Habitat Loss and the Threat of Extinction and Cultivation and Horticulture, Appendix, Glossary, Bibliography, Index.

This 1,399-page work contains 751 spectacular images. One-hundred-twenty species of *Nepenthes*, plus five incompletely diagnosed taxa are recognised, along with *Cephalotus follicularis*. Several of the species documented in this work have been discovered only very recently and, in many cases, the photographs presented in this work are among the first to be published. Examples include *N. argentii, N. attenboroughii, N. bellii, N. bokorensis, N. burkei, N. copelandii, N. danseri, N. deaniana, N. gracillima, N. kampotiana, N. klossii, N. kongkandana, N. mantalingajanensis, N. masoalensis, N. micramphora, N. mindanaoensis, N. mira, N. naga, N. paniculata, N. papuana, N. peltata, N. pilosa, N. pitopangii, N. surigaoensis, N. tenax, N. tenuis, N. tomoriana, N.* sp. Trang, *N.* sp. Phanga Nga, *N.* sp. Sulawesi, *N.* sp. Misool and *N.* sp. Papua. A newly discovered taxon from the Philippines, **Nepenthes micramphora** V. Heinrich, S. McPherson, Gronemeyer & Amoroso, is formally described in the Appendix and introduced here for the first time."

David Miller, Richard Warren, Izabel Moura Miller, and Helmut Seehawer. 2008. **The Organ Mountain Range: Its History and Its Orchids.** (ISBN 978-85-60217-01-4, hbk.). Editora Scart, Nova Friburgo, RJ, BRAZIL. (**Orders:** www.orchidconservationalliance.org). $95.00, 541 pp., 315 orchid photos, 228 water colors, 602 species described, 8" × 11".

From the Publisher: Over ten years, the authors criss-crossed the Organ Mountain Range looking for fragments of original forest in an area which had been devastated by the coffee and railway booms of the previous centuries. What they found will fascinate orchid lovers and

environmentalists alike. Small, inaccessible fragments—forest oases—still hold populations of plants that were abundant in precolonial time. And from the priceless comprehensive data they collected and present, the authors are able to reconstruct what the original pristine forest must have looked like when Darwin was there.

MISSOURI BOTANICAL GARDEN PRESS (ST. LOUIS, MISSOURI)

Peruvian Flora

Rodolfo Vásquez Martínez, Rocío Rojas Gonzáles, and Henk van der Werff, eds. 2010. **Flora del Río Cenepa, Amazonas, Perú. Volumen 1. Introducción, Pteridophyta, Gymnospermae y Angiospermae (Acanthaceae–Fabaceae); Volumen 2. Angiospermae (Gentianaceae–Zingiberaceae).** (ISBN 978-930723-93-1 [vol. 1]; 978-930723-94-8 [vol. 2], hbk.). *Monographs in Systematic Botany from the Missouri Botanical Garden*, Volume 114 (ISSN 0161-1542). Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $140.00 (2 vols.), 1,568 pp., illus., 7" × 10".

The *Flora del Río Cenepa, Amazonas, Perú* includes 3504 species in 1046 genera and 181 families; families, genera, and species are alphabetically arranged. Identification keys (indented) are provided for families, genera, and species; brief descriptions are given as well as notes on habitat preference. Common names—when known—are given in Spanish and Aguaruna (language of the indigenous people). This is a resourceful flora for a little-known botanical area of the world. Some 414 line drawings of plants enhance the flora. Highly recommended even at the $140.00 price tag, but for 1,568 pages, that is a pretty good bargain.

Flora of China

Wu Zhengyi and Peter H. Raven, Co-chairs of the editorial committee, Hong Deyuan, Vice co-chair of the editorial committee. 2009. **Flora of China Illustrations. Volume 7, Menispermaceae through Capparaceae.** (ISBN 978-930723-88-7, hbk.). Science Press, 16 Donghuangchenggen North Street, Beijing 100717, CHINA and Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $90.00, 520 pp., illus., 8¾" × 11¼".

From the Publisher: "Volume 7 of the illustrations series is devoted to 11 plant families; many of them are of economic and horticultural importance, and almost all of them are sources of medicine. Menispermaceae provide medicines, including the drug curare, and rattan; Illiciaceae are used for timber, ornamental plants, medicine, culinary spices, and perfume; Schisandraceae are known for their ornamental plants, medicine, fruit, fibers for rope, and volatile oils; Magnoliaceae supply medicine and ornamental plants; Calycanthaceae are used for horticulture, medicine, and tea; Myristicaceae are known for nutmeg and mace, fat used for candle making and industry, and medicine; Lauraceae provide cinnamon, bay leaves, camphor, medicine, timber, fruits, and oil used for perfumes; Hernandiaceae are used for timber and medicine; Papaveraceae supply medicine, including opium, edible seeds, oils used in soap manufacture, and ornamental poppy plants; Cleomaceae have horticultural and medicinal uses; and Capparaceae furnish us with capers and garden plants."

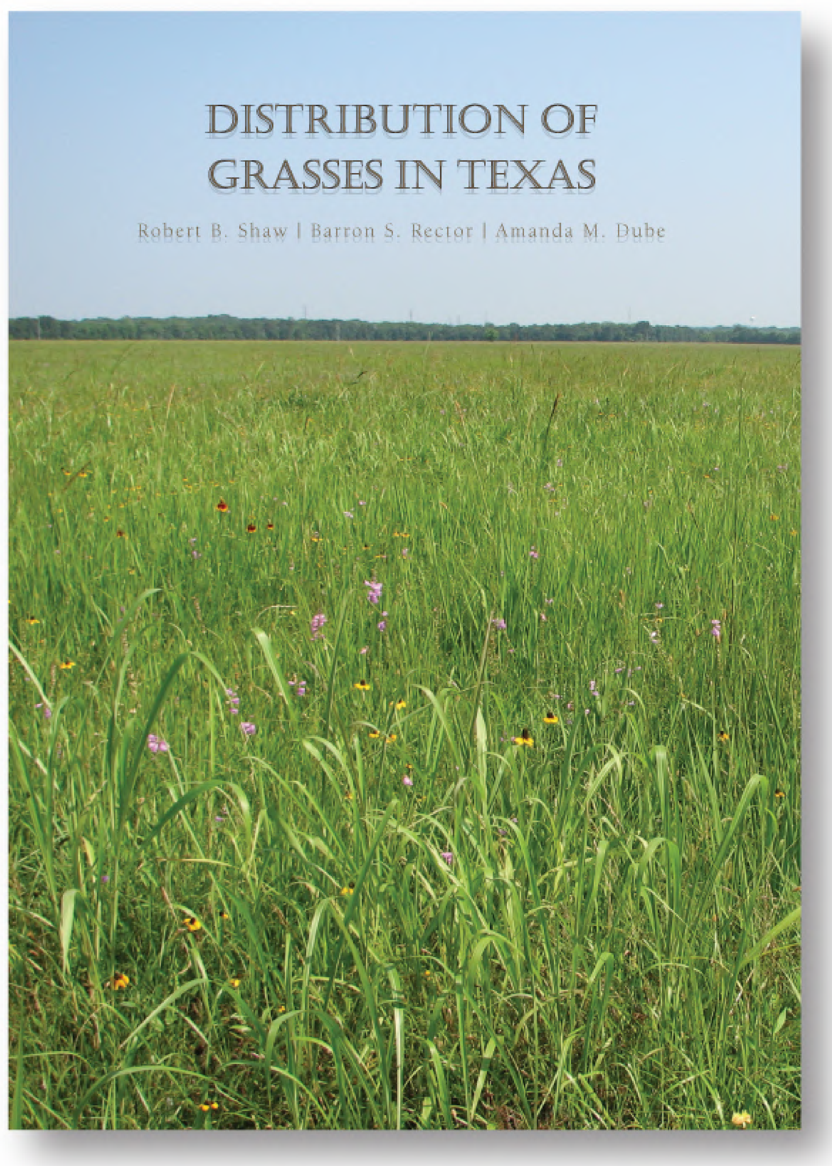
The illustration volumes of the *Flora of China* are incredibly useful to botanists and other users of botanical information.

Wu Zhengyi and Peter H. Raven, Co-chairs of the editorial committee, Hong Deyuan, Vice co-chair of the editorial committee. 2009. **Flora of China: Volume 25, Orchidaceae.** (ISBN 978-930723-90-0, hbk.). Science Press, 16 Donghuangchenggen North Street, Beijing 100717, CHINA and Missouri Botanical Garden Press, P.O. Box 299, St. Louis, Missouri 63199-0299, U.S.A. (**Orders:** www.mbgpress.org). $125.00, 570 pp., illus., 8¾" × 11¼".

From the Publisher: This volume entirely comprises the orchid family, or Orchidaceae, with 1,388 species in China, of which 494 are endemic, i.e., found nowhere else on Earth. The orchids of China include wild relatives of the source of the economically important vanilla pod, as well as the well-known cultivated genera *Cymbidium* and the slipper orchids, *Cypripedium* and *Paphiopedilum*. China has hundreds of other horticulturally important orchid species in genera such as *Bletilla*, *Bulbophyllum*, *Calanthe*, *Coelogyne*, *Dendrobium*, *Phalaenopsis*, *Pleione*, and *Vanda*. This volume is the only fully comprehensive and up-to-date, English-language account of the wild orchids of China.

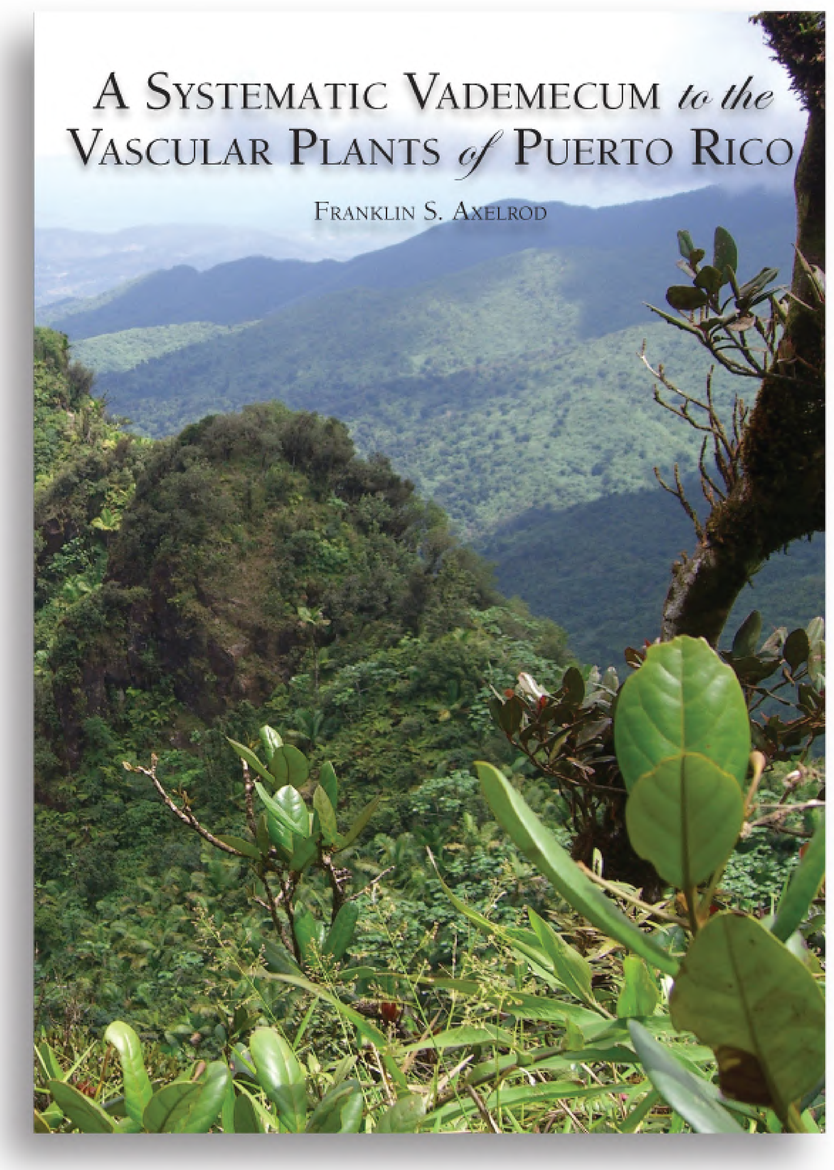
J. Bot. Res. Inst. Texas 5(1): 396. 2011

New Titles from the BRIT Press

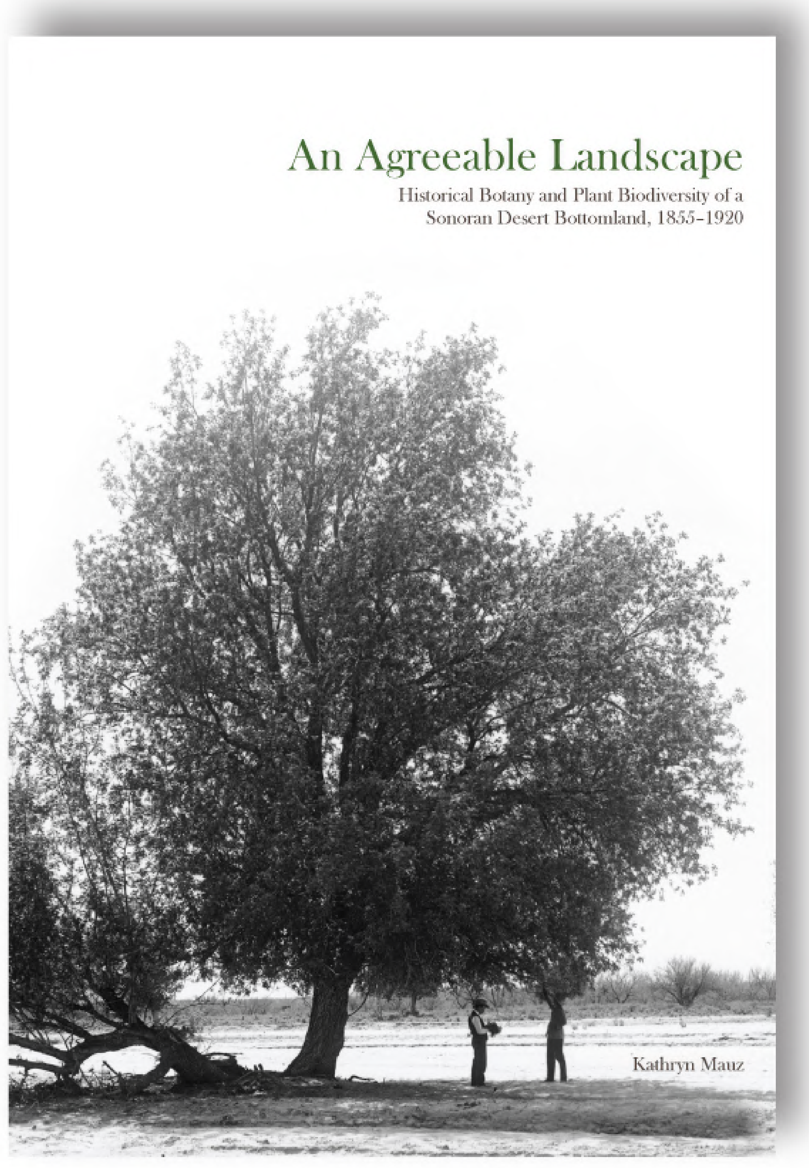


Distribution of Grasses in Texas is a compilation of information about the distribution of grasses in the 12 ecoregions and 254 counties of Texas. We found 721 species reported for the state and over 19,000 county distribution records. Featured in the book are a checklist of species by ecoregion, summaries of the number of documented species per county, and the number of counties where the top 101 species have been collected.

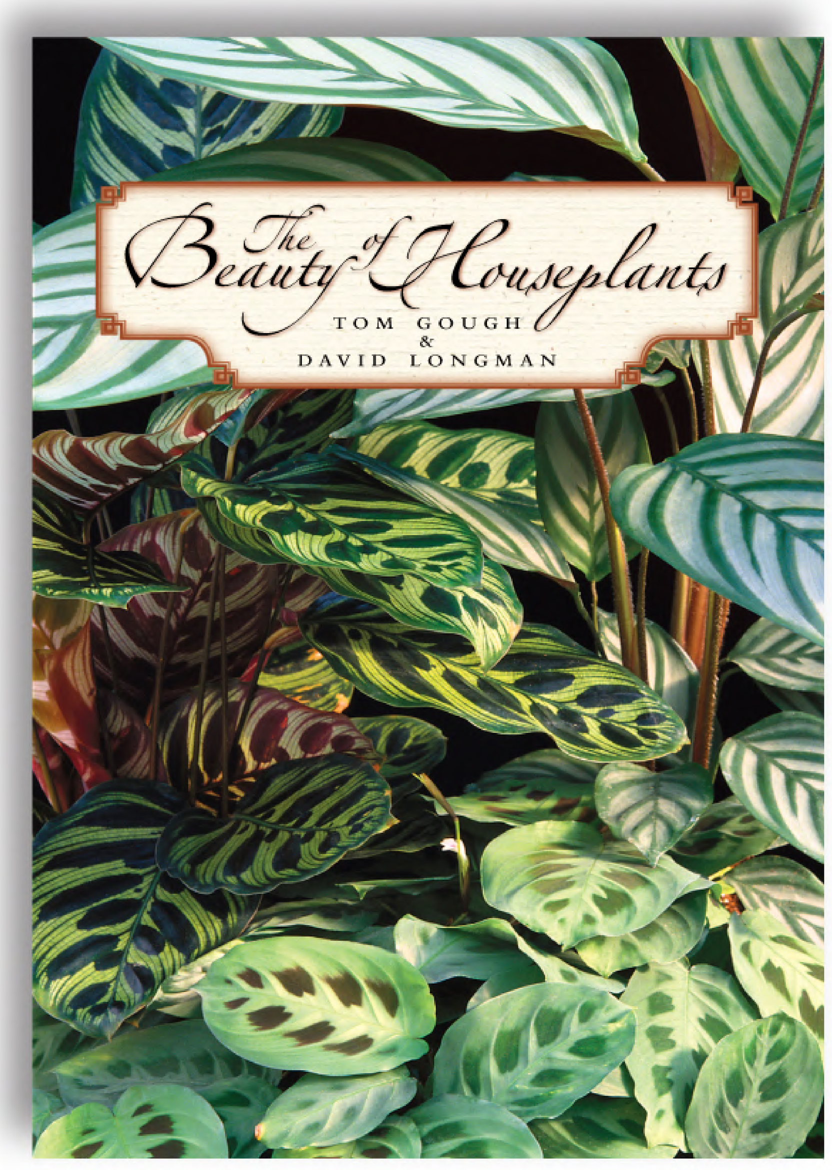
The largest parts of the book are two major lists. The first list is a record of grass species for each county; the second, documents the counties where a particular species has been collected. Data presented clearly indicates that the Poaceae, the most economically important of all plant families, is poorly collected across the state. Distribution of cultivars, ornamentals, and noxious or invasive weedy species, as well as numerous native perennial taxa, are poorly documented. Even common species need collecting. The authors hope that this work will stimulate collection of Texas grasses, and that specimens will be properly preserved in Texas herbaria.



Have you ever wondered where a Puerto Rican plant grows, when it flowers, where it comes from? Well, *A Systemtic Vademecum to the Vascular Plants of Puerto Rico* is a checklist of the vascular plants presently found growing in the wild on the island. This book will be an invaluable aid to botanists, ecologists, foresters and any one else interested in the flora of Puerto Rico. Here you will find the distribution of vascular plants within the island provided according to a novel scheme that incorporates both broad physiographic areas and specific geographical sites. These are both described in the text and illustrated by three maps. You will also find useful information on the times of flowering, fruiting, and spore production for each plant and also references for each one to recent monographs on Puerto Rican plants where a fuller description of each can be found.



An Agreeable Landscape: Historical Botany and Plant Biodiversity of a Sonoran Desert Bottomland, 1855–1920 is an accounting of plant life in the Santa Cruz and Rillito valleys of the Tucson Basin. Primary documents, historical narratives, and more than 1200 dried plant specimens are the foundation for this exploration of floristic richness, bottomland habitats, and ecological change. Over time, a convergence of cultural, political, and scientific currents at Tucson—arguably the seat of the Santa Cruz watershed—have made this the best-documented riparian ecosystem in the Sonoran Desert for this time period. This original compilation affords a vantage point from which to view the historic bottomland among the spectrum of riparian conservation in the region today, as well as to inform those ongoing efforts in a watershed that, even diminished, remains a biological resource of international importance.
***For a review of this title see page 218 of this issue.**



The Beauty of Houseplants is set apart from the normal houseplant care book by being a total delight to look at. The illustrations of over 70 houseplants are in themselves artistic and stunning, capturing the extraordinary variety and beauty of temperate plants with a detailed guide to their individual care and how to put right what goes wrong. The susceptibility of each plant to pests and diseases is dealt with separately and in detail with a chapter on their identification and how to deal with them. There is a section showing how to choose plants for each room of the house, depending on the amounts of heat, light and humidity. A potted history of how houseplants were discovered from all over the world and a chapter on propagation make this one of the most delightful reference books ever created on the subject.

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Journal of the Botanical Research Institute of Texas

The *Journal of the Botanical Research Institute of Texas*, formerly called *Sida, Contributions to Botany*, publishes research in classical and modern systematic botany—including studies of anatomy, biogeography, chemotaxonomy, ecology, evolution, floristics, genetics, paleobotany, palynology, and phylogenetic systematics. Geographic coverage is global. Articles are published in either English or Spanish; an abstract is provided in two languages. All contributions are peer reviewed and frequently illustrated with maps, line drawings, and full color photographs.

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The journal is published twice yearly in a multiple topic format and provides information to scientists, professionals, and the general public for research, education, and cultural enhancement. All articles are indexed and abstracted in print and/or electronic form by the following: AGRICOLA Database (National Agricultural Library); Applied Botany Abstracts; Biosciences Information Service of Biological Sciences (BIOSIS); Current Awareness in Biological Sciences (CABS); The Kew Record of Taxonomic Literature; Natural Products Alert (NAPRALERT); and Referativnyi Zhurnal (Abstracts Journal of the Institute of Scientific Information of the Republic of Russia).

Lloyd H. Shinners, whose herbarium and library were the basis of the Southern Methodist University (SMU) legacy that became BRIT in 1987, founded the journal in 1962. **William F. Mahler** succeeded Shinners as SMU herbarium director in 1971 and inherited both ownership and editorship of the journal. Since 1993, it has been published by the Botanical Research Institute of Texas.

The current issue of the *Journal of the Botanical Research Institute of Texas* is available online at http://www.britpress.org.

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